Ecology of Reindeer on Hagemeister Island, Alaska

by

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ABSTRACT

The objective of this study was to investigate and characterize the factors driving the Hagemeister Island reindeer population. A total of 144 reindeer were introduced to Hagemeister Island in 1965 and 1967. The herd initially increased in size to about 1,000 head and then fluctuated around 800 animals. In 1991-1992, a moderate winter die-off of primarily adult bulls (> 90%) occurred. Adverse snow conditions and poor post rut conditions of bulls appeared to have facilitated the die-off. No conclusive evidence was found that the herd experienced effects of density-dependent food limitation despite poor winter lichen range. In 1993, conception was documented in calves and overall pregnancy rate was approximately 70%. Body size and condition was comparable to other arctic island reindeer herds. This suggests that reindeer on Hagemeister Island do not solely depend on lichen during winter but utilize other forages.

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Common Name	Scientific Name
Alaska Bog Willow	*Salix fuscescens*
Bigelow Sedge	*Carex bigelowi*
Bluejoint	*Calamagrostis canadensis*
Clustered Sedge	*Carex glarosa*
Crowberry	*Empetrum nigrum*
Diamondleaf Willow	*Salix pulchra*
Green Alder	*Alnus crispa*
Lichen spp.	*Cladina spp.*
Netleaf Willow	*Salix reticulata*
Northern Labrador Tea	*Ledum decumbens*
Water Sedge	*Carex aquatilis*

List of Animals

Common Name	Scientific Name
Bald Eagle	*Aquila chrysatetos*
Beaver	*Castor canadensis*
Black-legged Kittiwake	*Riss tridactyla*
Brown Bear	*Ursus arctos*
Common Eider	*Somateria millisima*
Common Murre	*Uria aalge*
Glaucous Gull	*Larus hyperborus*
Glaucous-winged Gull	*Larus glaucescens*
Harbor Seals	*Phoca vitulina*
Harlequin Duck	*Histrionicus histrionicus*
King Eider	*Somateria spectabilis*
Long-tailed Jaeger	*Stercorarius longicaudus*
Oldsqaw Duck	*Clangula hyemalis*
Pelagic Cormorant	*Phalacrocorax pelagicus*
Pigeon Guillemot	*Cephus columba*
Raven	*Corvus corax*
Red Fox	*Vulpes vulpes*
Sandhill Crane	*Grus canadensis*
Sea Otter	*Enhydra marina*
Steller's Eider	*Polystictastelleri*
Trumpeter Swan	*Olor columbianus*
Tufted Puffin	*Lunda cirrhata*
Walrus	*Odobenus rosmarus*
Willow Ptarmigan	*Lagopus lagopus*

List of Abbreviations and Acronyms

USDA-	United States Departement of Agriculture
SCS	Soil Conservation Service
BIA	Bureau of Indian Affairs
BLM	Bureau of Land Management
US-F&WS	United States Fish and Wildlife Service
g	gram
kg	kilogram
mm	millimeter
cm	centimeter
m	meter
km	kilometer
ha	hectare
n.s	not significant at the 5% significance level
*	significant at the 5% significance level

List of Model Symbols

Symbol	Function
+	addition
-	subtraction
*	multiplication
/	division
c	current
p	previous
π	pi
y	intercept
x	variable

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Chapter 1
Introduction

In 1965 and 1967, the Bureau of Indian Affairs (BIA) introduced reindeer to Hagemeister Island, Alaska. The objective of this introduction was to provide Native Alaskans with the opportunity to establish a reindeer herding industry and an alternative source of meat (Stern et al. 1980). The island differs from the mainland in an absence of indigenous large predators. The only population management of the herd was by Native herders from the village of Togiak. However, routine seasonal management and harvest of animals on Hagemeister Island has been compromised by remoteness, inclement weather conditions, and the difficulty of scheduling seasonal management activities with the subsistence lifestyle[1].

Historical Background

A total of 144 reindeer from Nunivak Island were introduced to Hagemeister Island in 1965 and 1967. The Hagemeister Island reindeer herd increased steadily in size until the 1970's. By 1971, the population had reached 1,011 animals. During the 1970's, the population fluctuated from an estimated 590 to 953 animals (Swanson and LaPlant 1987). Concerns about overgrazing were expressed in 1973 by the Bureau of Land Management (BLM). Recommendations were made to reduce the size of the privately-owned herd to 450 animals[2]. In 1980, the responsibility of land management for Hagemeister Island was transferred by Congress to the U.S. Fish and Wildlife Service (US-F&WS). In the mid-1980's,

[1]1987 letter by D. Laplant to J. Martin (in BLM and US-F&WS files).
[2]1973 letter by J. Merrick to Messrs. Bavilla, Christian, and Gosuk (in BLM and US-F&WS files).

spring aerial surveys conducted by US-F&WS to assess range conditions and census reindeer numbers verified the concern of overgrazing. In 1986, a range survey was conducted by the USDA-Soil Conservation Service (USDA-SCS) to assess lichen production and range condition. The study concluded that 80% of the lichen range was in poor condition and appeared to be declining (Swanson and LaPlant 1987). Swanson and LaPlant (1987) suggested either removal of the entire herd or reduction of breeding herd to either 200 or 50 head depending on the intensity of planned herd management. In 1990 and 1991, the herd size was estimated to be approximately 1,530 and 952 animals, respectively. During the late winter 1991-1992, a die-off of approximately 300 reindeer, predominantly adult bulls occurred on Hagemeister Island (Stimmelmayr and Renecker 1992; see Chapter 3).

It has been a widely accepted view that insular herbivore populations are largely limited by food resources, climatic fluctuations, prevalence of disease and/or human harvest (Klein 1968; Leader-Williams 1988; Reimers 1977, 1982, and 1983; Scheffer 1951). Changes in lichen availability and/or production concomitant with extreme weather conditions have been implicated as the cause of population fluctuations in several high arctic insular *Rangifer* populations, for example, on St. Matthew Island (Klein 1968), the Pribilof Islands (Scheffer 1951), and Coats Island (Gates et al. 1986).

Theories Behind Population Dynamics

A population is described as a group of animals composed of individuals of a species inhabiting a certain space-time continuum, and reproducing, if reproductively active (Soule 1987). A population is defined by the biological parameters of: birth, mortality, immigration, and emigration rates

(Soule 1987; Owen-Smith 1988). The natality rate of a population is a function of: age-specific fecundity rate, birthing and gestation interval, litter size, and genotype. Recruitment rate of a population is a function of natality rate and progeny survivorship (Soule 1987). Declines in the recruitment rate of *Rangifer* populations have been attributed to low subadult (< 2 years) conception rates (Skogland 1985b, 1990), delayed maturity (Leader-Williams 1988), breeding in alternate years (Reimers 1983; Thomas 1982), and low calf survivorship (Doerr 1980; Skogland 1984). Mortality rate in a population is characterized as either compensatory or additive (Miller and Ballard 1992). Only additive mortality increases the overall mortality rate in a population, while compensatory mortality simply replaces an existing cause of mortality by another.

Abundance of large herbivores appears to be for the most part affected by extrinsic mechanisms such as food resources, predation, weather, and diseases (Caughley 1970; Owen-Smith 1988; Riney 1964). Intrinsic mechanisms such as individual behavioral and physiological responses operate in small mammal populations (Lee and McDonald 1985). These mechanisms described above influence animal populations by modifying recruitment and mortality rates. When neither immigration nor emigration occurs, they are the single determinants of the size of any given animal population (Caughley 1970). A change in these population parameters results in concomitant fluctuations in size. These biological parameters and their respective population may be either density-dependent or independent, or both. Density-dependent populations change as a function of population density (Skogland 1985b). For reasons of consistency with respect to use of terminology, establishable density-dependent mechanisms are named "regulatory" factors. The

term "limiting" can be applied to denote factors that are either density-dependent or independent (Messier 1989).

What Drives Population Dynamics?

If a herbivore population living in a predator-free environment is subjected to limiting factors, the pattern of change takes the form of either dampened or divergent oscillations which lead to the extinction of the herbivore, plants, or both (Owen-Smith 1988). Food resources, weather, and diseases are considered to be the main limiting factors for predator-free herbivore populations. An eruptive oscillation is characteristic of an expanding population at low densities in a favorable habitat (Caughley 1970). This type of population usually stabilizes at a lower density than obtained during earlier stages of eruption (Riney 1964). The propensity of an expanding herbivore population to overshoot ecological carrying capacity has been explained as a function of the high proportion of young in the expanding population (Riney 1964) and/or the non-linear dependence of population parameters such as fecundity and mortality on population density (Owen-Smith 1988). On the other hand, simulation models have indicated that the possibility of dispersal and/or influence of predators can dampen population fluctuations. Individuals are removed before starvation occurs and population density is suppressed below the saturation level set by nutritional limitations (Owen-Smith 1988). For insular populations of herbivores, extreme weather conditions and disease could limit population growth. Studies with high-arctic *Rangifer* populations have emphasized the effect of weather on winter food availability and as result higher mortality rates due to starvation (Gates et al. 1986; Reimers 1977, 1982). Extreme weather can also affect progeny survival by:

increasing perinatal mortality due to hypothermia (Chetkiewicz 1993; Hart et al. 1961; Lentz and Hart 1960; Nowosad 1972), or lower birthweights, because of poor winter forage conditions for the pregnant female (Adamzweski et al. 1987b; Jacobsen and Skjenneberg 1975). Diseases (Skjenneberg and Slagsvold 1968; Zhigunov 1968) and accidental deaths including drowning, cliff falls, and avalanches have been cited as main causes of mortality in some *Rangifer* populations. For most *Rangifer* populations, the impact of disease is not continually present. Prevalence of disease is generally low and sporadic. Depending on the topography of the area inhabited by *Rangifer*, accidental deaths rates can be substantial (Leader-Williams 1988; Scheffer 1951). For example, 23% of the total winter mortality of reindeer calves on South Georgia Island was attributed to cliff falls (Leader-Williams 1988).

In conclusion, weather and disease mechanisms could dampen population fluctuations if they reach sufficient magnitude to be limiting. However, from the introduction of *Rangifer* to island settings throughout the world, one has to conclude that with the exception of St. George and possibly Hagemeister Island, introductions of reindeer either failed or entered an eruptive oscillation (Leader-Williams 1988). Ecological differences such as climate, vegetation, and island topography have been thought to be the reason why the St. George Island reindeer herd experienced a dampened fluctuation (Scheffer 1951).

Density-Dependent Resource Limitations of High-Arctic *Rangifer*

Winter Range

At high latitudes, carrying capacity is essentially dichotomous with only summer and winter components (Klein

1965, 1968; White et al. 1987). Winter range carrying capacity is governed by animal numbers in a density-dependent manner, and snow and/or ice crust characteristics that determines forage accessibility. Studies have shown that winter snow and ice can reduce the food supply of *Rangifer* from 1 to 5% of the total summer forage biomass (Adamczewski et al. 1988; Bergerud 1974). Because "cratering" for forage is an energetic cost (Helle 1984; Thing 1977) to reindeer during the winter nadir, they strategically select areas characterized by shallow and soft snow (Gheller 1984; Fancy and White 1985). Snow depth > 50-70 cm and hardness > 10 000 g/cm^2, depending on the habitat type, impedes cratering by *Rangifer* (Collins and Smith 1991; Miller et al. 1982; Skogland 1978; White et al. 1981; Thing 1977). The winter range carrying capacity is considered to be the limiting factor for the upper size of *Rangifer* populations (Klein 1968; Tyler 1987).

The winter food habit of most *Rangifer* populations is characterized by the predominant use of lichens (Bergerud 1977; Klein 1982 ; Luick 1977; Miller 1976; Skjenneberg and Slagsvold 1968; Zhigunov 1968). There are three primary reasons for this particular feeding ecology. First, *Rangifer* presumably evolved from a grassland feeder to fill a lichen-based northern food niche essentially unoccupied by other herbivores (Andreev 1984; Klein 1982; Zhigunov 1968). The high digestibility of lichens and ability of *Rangifer* to locate lichen beneath the snow cover is thought to reflect this co-evolutionary relationship. Secondly, winter reindeer range in alpine and arctic regions is greatly influenced by snow and ice conditions. Thus foraging by reindeer is restricted to areas: accessible; windswept; and/or with limited snow fall (Adamzweski et al. 1988; Klein 1959; Tyler 1987). By nature of their exposure, these areas are flats

and ridges that support mainly xerix plant communities such as lichens and willows. Thirdly, lichens constitute the dominant plant biomass in northern tundra ecosystems and particularly, in xeric habitats (Klein and Vlasova 1991). Consequently, lichens are the primary food in most arctic and alpine habitats occupied by reindeer and caribou because of their widespread distribution and relative abundance. The winter utilization of lichens by *Rangifer* has led to the widely held conclusion of exclusive dependence on this forage species. This has resulted in many *Rangifer* range studies, throughout the circumpolar distribution of *Rangifer* that have focused on estimation of lichen abundance and biomass (i.e. Palmer and Rouse 1945; Swanson and Barker 1991). Examples of high-arctic *Rangifer* populations, mainly insular, being productive while inhabiting over-grazed lichen or lichen-free range (Finstad and Renecker 1991; Leader-Williams 1988; Parker 1978; Staaland et al. 1991; Thing 1984) have challenged this hypothesis. In lichen-free habitats, graminoids or moss constitute the main food item in the winter diet of *Rangifer* (Leader-Williams 1988). A similar trend of increasing habitat niche breadth has been observed for continental *Rangifer* populations that inhabit lichen-depleted winter ranges (Skogland 1984). This suggests that the key to species utilization by *Rangifer* lays in the relative availability of forages as proposed by Bergerud (1977) rather than dependence on a particular diet.

Summer Range

Carrying capacity of the summer range is predominantly influenced by animal numbers in a density-dependent manner, and density-independent factors such as catastrophic climatic events that effect plant phenology. Because arctic summers are of short duration, summer forage

is generally only available for a brief period of time. Protracted availability of forage, however, can occur. Extreme topographic habitat variations such as altitude, exposure, and slope results in variable phenological progression of plants (Klein 1965; Bergerud 1977). In alpine and arctic regions, summer forage is of high nutritive quality (crude protein 10% - 25%) (Bergerud 1977) and is associated with the rapid growth rates of arctic herbivores (Klein 1965, 1968). The high nutritive quality of arctic forage has been attributed to: long daily periods of plant growth in response to greater solar insolation, brief periods of darkness and respective brief periods of catabolic losses by plants, low ambient temperatures during the night which reduce the physiological decline of carbohydrate levels in plants, and short duration of vegetative stages resulting in rapid growth and high nutritive content (Klein 1965, 1970). Animal performance, such as body and antler growth (Klein 1964; White 1983), reproduction (Thomas 1982), lactation (White 1983; Reimers 1983b), calf survival (Skogland 1985b), and early-winter survival (Reimers 1977, 1982, 1983) are thought to be more strongly related to summer range conditions. The summer food habits of *Rangifer* are characterized by the predominant use of green vascular plants and mushrooms (Bergerud 1977; Luick 1977; Skjenneberg and Slagsvold 1968; Zhigunov 1968). This suggests that *Rangifer* are opportunistic feeders during the summer and maximize utilization of high quality forage (Skogland 1989).

Physical and Reproductive Attributes of Reindeer

Reindeer exhibit distinct circannual patterns of growth, weight change and body composition, food intake, and reproductive activity (White et al. 1981, 1987). This strong

seasonal response is viewed as an adaptive strategy to cope with change in quantity and quality of forage, climatic extremes, and to ensure reproductive success of the species. Regulation of these circannual cycles is thought to be a function of endogenous rhythms that are entrained by photoperiod (Ryg 1982; Ryg and Jacobsen 1982).

Body Weight and Composition

Growth and replenishment of body tissue reserves occur only during the short arctic summer. Spring growth and body composition are initially characterized by deposition of protein and hydration of muscle tissue. Later in the season, lipogenesis and deposition of fat predominate (Allay-Chan 1991). In males, maximum deposition of fat is attained by early fall prior to the breeding season. During rut, most of the fat reserves in males are depleted. This suggests that the main role of the fat reserves in males is to enhance reproductive success (Leader-Williams 1988; Tyler 1987). Females continue to deposit fat until late fall (Adamzweski et al. 1987b; Leader-Williams 1988; Tyler 1987). However, the luxury of reproduction in the female also remains closely linked to body condition. Thus females must attain a set point condition before breeding will occur (Adamzweski et al. 1987b; Allay-Chan 1991; Tyler 1987). The delayed mobilization of fat reserves until the last trimester in pregnant females suggests that the principal role of fat reserves in female reindeer may be to supplement their food intake during late pregnancy and/or early lactation (McEwan and Whitehead 1970; Tyler 1987; Tyler and Blix 1990). During the winter period, reindeer and caribou experience a growth stasis. However, Ryg and Jacobsen (1982) observed that the growth stasis in calves could be reversed if calves were fed concentrate *ad lib*.

Male reindeer approach their lowest body weight towards the end of winter, while pregnant females will shortly after parturition (Leader-Williams 1988). Male reindeer have greater absolute weight loss and at a greater rate than females (Tyler and Blix 1990). The difference in mobilization of fat and other body reserves might explain the timing and sex-specific mortality rates observed in free-ranging reindeer herds that are food limited. Mortality rate in males is highest during the winter period, shortly after the rut, while pregnant females experience highest mortality rate during the lactation period (Klein 1968; 1970; Leader-Williams 1988; Reimers 1977 and 1982).

The magnitude of seasonal weight change has varied within and between *Rangifer* populations. The observed variations have been attributed to differences in: breeding stock (Palmer 1934; White and Hauer 1989), spring and summer range quality (Klein 1968; Kumpula and Nieminen 1992; Reimers 1983b), and presence of harassment by predators and insects (Reimers 1980). The magnitude of compensatory gain by autumn (maximum body weight) is proportional to the deviation of spring body weight (minimum) from the peak autumn set-weight (Ryg 1982). In *Rangifer*, compensatory gain in spring resulted in a greater propensity to deposit protein (Allay-Chan 1991). Protein deposition is associated with more water than fat deposition (ARC 1984). This suggests that hydration of muscle tissue contributes to the rapid spring weight change in *Rangifer* (Allay-Chan 1991). Several hypothesis have been advanced to explain the underlying mechanism for compensatory gain. Studies with wild and domestic ungulates suggest that: (1) high voluntary intake (Ryg 1982), (2) uncoupling of metabolic rate and intake prior to green-up as a preparatory measure (Hudson and Christopherson 1985), (3) use of heat increment of feeding for thermoregulation

(O'Donnovan 1984), and (4) hydration of protein which is less energy expensive than synthesis of fat (ARC 1984) results in an increased efficiency for gain. Compensatory gain in northern ungulates is thought to be an adaptive response to the extreme environmental conditions under which they live (Price and White 1985). This suggests that the ability to achieve set point weight during a short growth pulse ensures survival and reproduction (O'Donnovan 1984; Hudson and Christopherson 1985; Price and White 1985)

Reproductive Biology

Reindeer and caribou are a seasonally polyestrus species. The reproductive period is synchronous which results in a narrow birth window of 2-3 weeks (Dauphine and McClure 1974; Leader-Williams 1988; Roine 1974). The onset of the breeding season has varied within and between *Rangifer* populations (Bergerud 1980; Leader-Williams 1988; Holthe 1972). These variations have been attributed to differences in latitude, genetic stock, and body condition of females (Leader-Williams 1988; Skogland 1985b, 1986, 1990; White and Luick 1984). The variation in the reproductive performance of female reindeer, both in age of first breeding and age-specific pregnancy rate between the various sub-species, has been attributed to differences in body condition (Cameron et al. 1993; Dauphine 1976; Leader-Williams 1988; McEwan 1963; Reimers 1983a; Roine 1974; White et al. 1981). Early sexual maturity and high pregnancy rates are thought to reflect good nutritional food and/or body condition (Palmer 1934; Ropstad et al. 1991; Skjenneberg and Slagsvold 1968). Female reindeer attain physiological puberty usually as yearlings. However, they can conceive as calves (Roine 1974; Palmer 1934). Studies in Norway have shown that onset of puberty and the pregnancy rate in

reindeer calves are strongly correlated with peak autumn body weight (Ropstad et al. 1991). Pregnancies in reindeer calves with an autumn body weight > 50 kg were common. This suggests that there is a lower limit of body weight (fat reserves) below which pregnancy is not possible.

Reindeer usually produce one calf, but twinning can occur (Godkin 1986; McEwan and Whitehead 1971). Average length of gestation period is estimated to be 220 days. However, considerable variations can occur. Length of gestation has been reported to range from 208 to 238 days (Bergerud 1975; Dott and Usi 1973; Flerov 1952; Palmer 1934; McEwan and Whitehead 1971). For most studies, the measurement of gestation length has been derived by subtracting mean dates of estrus and birth. The onset of estrus can be estimated on the basis of behavioral observations such as breeding activity or with ovarian analysis. However, both techniques are affected by sample size, repeated cycling, or occurrence of silent estrus. Thus differences may be linked to method of estimation. On the other hand, several authors have proposed the hypothesis that female reindeer have a physiological plasticity and are able to modify gestation length possibly in response to environmental conditions such as green-up (Bergerud 1975; Epsmark 1980). This would suggest that the above reported range for gestation length may be accurate for *Rangifer*.

Either short (10-12 days) or long (24 days) estrus cycles can occur in reindeer (Bergerud 1975; Dott and Utsi 1973; McEwan and Whitehead 1971). Silent estrus (no overt signs) has been reported to occur in caribou, but not in reindeer at the start of the breeding season (Bergerud 1975; Dauphine 1976; McEwan 1963; McEwan and Whitehead 1980). Recurrent cycling is thought to occur in the case of conception failure (McEwan 1963; McEwan and Whitehead 1971). In the

majority of female reindeer, only one ovulation occurs per cycle, but secondary ovulations can occur (Roine 1974; Leader-Williams 1988). Ovulation results in the formation of a corpus luteum. Corpus luteum post conception (CLPC; synonym secondary corpus luteum) is usually smaller in size, but otherwise identical in appearance to the primary corpus luteum (CLP) (Dauphine 1978; Leader-Williams 1988). In case of conception, luteal structure(s) initially increases in size. These corpora lutea persist throughout the gestation period and are thought to be the main source of progesterone in reindeer, which maintains pregnancy (McEwan 1963). After parturition and/or in case of conception failure, luteal structures regress and are presumably preserved in the ovary in form of fibrous pigmented scars for an extended period of time (Dauphine 1978; Leader-Williams 1988; McEwan 1963). Counts of numbers in luteal scars have been used to determine productivity in *Rangifer* (Dauphine 1978; Leader-Williams and Rosser 1982; Leader-Williams 1988; McEwan 1963; Skoog 1968).

Is the Reindeer Population on Hagemeister Island Limited by Winter Lichen Range in a Density-Dependent Manner?

During the field investigation of the 1991-1992 winter die-off an apparent delay in calving time of reindeer on Hagemeister Island was observed (Stimmelmayr and Renecker 1992). Peak calving as indicated by aerial surveys was between late May and early June. This was an unusual phenomena, in that normal calving of reindeer on the Seward Peninsula, Alaska is between late April and early May. The reproductive cycle of female reindeer and caribou is strongly correlated to body condition and size (Cameron et al. 1993; Thomas 1982; Ropstad et al. 1991). Female reindeer must attain a certain threshold weight (> 50 kg) prior to

the rut before breeding will occur (Allay-Chan 1991; Tyler 1987). Thus the apparent delay in calving time could suggest that female reindeer on Hagemeister Island do not reach set-target body weights in autumn, but at a later date due to limited food resources. This would result in a later breeding season and subsequently later calving season. If this is true than the late entry of females into the rut may explain the largely male die-off during winter 1991-1992. The onset of rut in mature male reindeer and caribou is thought to be mainly cued by photoperiod (Ryg 1982; Tyler 1987; Tyler and Blix 1990). Thus male reindeer would enter rut by late August. During the rut, male reindeer exhibit reduced feed intake and deplete their fat stores (Tyler and Blix 1990). This coupled with the additional intense rut later in autumn would place males in a precarious body condition, in that a brief period of food shortage caused by adverse climatic conditions could result in death due to malnutrition.

Other studies conflict on whether winter lichen range limits *Rangifer* populations, (Leader-Williams 1988; Skoog 1968; Skogland 1985b, 1986). It appears that area specific climatic conditions and topography, floral diversity and productivity, possibility of range expansion and dispersal, and accessibility of winter forage other than lichens are the essential modifying factors by which *Rangifer* populations can exist in lichen-free habitats. If I assume that reindeer on Hagemeister Island are not limited by winter lichen range then the apparent delay in calving time may be linked to their breeding history. However, if the reindeer population on Hagemeister Island was limited by winter lichen range than I should be able to demonstrate other density-dependent effects of food limitation such as decreased juvenile survival, lowered subadult fecundity,

body size decrements, and increased male mortality. This thesis research addressed the hypothesis that the reindeer population on Hagemeister Island was not limited by winter lichen range in a density-dependent manner, but foraged on other plants throughout the year.

Objectives

The main objective of this thesis was to investigate and characterize the factors limiting the reindeer population on Hagemeister Island. The study is summarized in five chapters that address the specific objectives to:

Chapter 2: describe the characteristics of the study area with respect to island topography, climate, vegetation, and native wildlife;

Chapter 3: document the 1991-1992 winter mortality of reindeer on Hagemeister Island and to explore possible causes;

Chapter 4: describe the reproductive characteristics of reindeer on Hagemeister Island;

Chapter 5: determine seasonal body composition of reindeer on Hagemeister Island; and

Chapter 6: describe the dynamics of the reindeer population on Hagemeister Island from its introduction and to develop a computer-based simulation model intended to illustrate the population dynamics of this population.

In each chapter an attempt was made to discuss findings with regard to the dynamics of this insular reindeer population. Chapter 7 integrates findings and assesses the management decision made for the reindeer population on Hagemeister Island.

Chapter 2
Study Area

Island Topography

Hagemeister Island is located in Bristol Bay of the Bering Sea at approximately 160° 54' west longitude and 58° 39' north latitude and about 530 km WNW of Anchorage, Alaska (Fig.2.1). It is part of the Alaska Maritime National Wildlife Refuge and currently under temporary management of the Togiak National Wildlife Refuge. The island is 37.4 km long by 11.3 km at its widest point and encompasses approximately 27,328 ha. The topography of the island is characterized by north-south ridges, which are intervened by low valleys. Elevations vary from sea level to 543 m at the south end of the island.

Climate

Weather records are not available for Hagemeister Island. On the basis of personal observations during this study and information obtained from residents of the village of Togiak, I have characterized the climate of Hagemeister Island. The climate is classified between maritime and continental. Summers are cool and humid with relatively few days above 20° C. Maximum precipitation occurs during late summer and autumn, while the driest period is early spring. The prevailing winds are from the north and southwest in summer and winter, respectively. During the winter months, freezing rains resulting in a thick ice cover appear to be quite common in the Togiak area. Gale force winds occur frequently during the early spring and autumn and particularly during the month of September (G. Carlos pers. commun. 1993).

Vegetation

Dominant vegetation types on Hagemeister Island (Table 2.1) include: (1) tall shrub (along drainage way), (2) tall shrub (hillside), (3) low shrub tundra (moist), (4) low shrub meadow (alpine), (5) low shrub lichen meadow, (6) sedge (wet meadow), and (7) beach dunes (coastal) (Swanson and LaPlant 1987; Swanson and Barker 1993). There are no trees on the island. Examination of vegetation sites in 1992 (Swanson and Barker 1993) revealed 93% of the transects were overgrazed and exceeded lichen utilization class 5 (Table 2.2). Class 5 is characterized by a > 76% disturbance of the lichen cover and trampling and/or cratering is evident. Utilization on sites dominated by vascular plants was slight and the conditions of these was estimated as good-excellent. Swanson and Barker (1993) ascribed average condition of vegetation types for 20 of the 23 island wide transect locations on the basis of either climax or potential plant production. Condition rating for vascular plant sites was rated good and poor for lichen sites, respectively (Table 2.3). Apparent trend of condition showed a decline for all lichen transects and static to improving on the vascular dominated transects. Erosion was not viewed as a problem (Swanson and Barker 1993). Areas of severe soil erosion (attributed to overgrazing), amounted to less than 3 ha. Invasion of weeds or significant shifts in plant composition by opportunistic plants had not occurred, however, mosses had become more dominant in some parts of Hagemeister Island (Swanson and Barker 1993).

Wildlife

Animal inhabitants include red fox, (*Vulpes vulpes*), and small rodents. Individual brown bears (*Ursus arctos*) have repeatedly been sited on the island. It is thought that they

may swim, presumably at low tide across Hagemeister Strait, (only 2 km wide), which separates the island from the mainland. According to Togiak residents approximately ten bears have been killed on the island by villagers over the last 20 years. During 1992 and 1993, two brown bears were sited on the island (M. Hinkes pers. commun. 1994). On the basis of tracks and direct observation, one bear was seen several times feeding on beached walrus (*Odobenus rosmarus*) carcasses (R. Stimmelmayr pers. commun. 1993; R. Doyle pers. commun. 1993). There is a wide variety of sea, shore, and songbirds. Species of birds observed during this study on Hagemeister Island are summarized in Table 2.4. Harbor seals (*Phoca vitulina*), and occasionally walrus (*Odobenus rosmarus*) haul out on the rocky beaches on the south end of the island. According to residents of the village of Togiak sea otters (*Enhydra marina*), and beavers (*Castor canadensis*) have also been sited on the island.

Fig.2.1. Location of Hagemeister Island, Alaska.

Table 2.1. Dominant plant species of vegetation types on Hagemeister Island[1].

Plant Species		Vegetation types[2]					
Common Name	Scientific Name	1	2	3	4	5	6
Alaska Bog Willow	*Salix fuscescens*						x
Bigelow Sedge	*Carex bigelowi*				x	x	
Bluejoint	*Calamagrostis canadensis*		x				
Clustered Sedge	*Carex glareosa*						x
Crowberry	*Empetrum nigrum*			x			
Diamondleaf Willow	*Salix pulchra*	x					
Green Alder	*Alnus crispa*	x	x				
Lichen spp.	*Cladina* spp.					x	
Netleaf Willow	*Salix reticulata*				x		
North.Labrador Tea	*Ledum decumbens*			x			
Water Sedge	*Carex aquatilis*						x

[1]Source: Swanson and LaPlant 1987

[2](1) tall shrub (along drainage way), (2) tall shrub (hillside), (3) low shrub tundra (moist), (4) low shrub meadow (alpine), (5) low shrub lichen meadow, (6) sedge (wet meadow).

Table 2.2. Classification of lichen utilization[1].

Class	Disturbance (%)	Comments
0-None	0	pristine
1-Trace	< 5	no trampling
2-Slight	5-25	slight grazing; no craters.
3-Moderate	26-50	same as 2, may have shallow craters in the mat.
4-Moderately heavy	51-75	lichen use apparent, top cropping evident; craters visible from a 6 meter distance.
5-Heavy	76-100	trampling and/or craters evident; adequate lichen remains for regeneration.
	Erosion (%)	
6-Severely heavy	< 25	craters extend through the mat; mineral soil and/or organic material exposed.
7-Severe	25-50	same as 6; lichen fragments are < 2 cm.
8-Extreme	50-100	same as 7, but lichen fragments not adequate for regeneration.

[1]Source: Swanson and Barker 1991

Table 2.3. Classification of average condition of vegetation types on Hagemeister Island[1].

Class	Condition (%)
poor	0-25
fair	26-50
good	51-75
excellent	76-100

[1]Source: Swanson and Barker 1993

Table 2.4. Species of birds observed on Hagemeister Island[1].

Common Name	Scientific Name
Bald Eagle	*Aquila chrysatetos*
Black-legged Kittiwake	*Riss tridactyla*
Common Eider	*Somateria millissima*
Common Murre	*Uria aalge*
Glaucous Gull	*Larus hyperborus*
Glaucous-winged Gull	*Larus glaucescens*
Harlequin Duck	*Histrionicus histrionicus*
King Eider	*Somateria spectabilis*
Long-tailed Jaeger	*Stercorarius longicaudus*
Oldsquaw Duck	*Clangula hyemalis*
Pelagic Cormorant	*Phalacrocorax pelagicus*
Pigeon Guillemot	*Cephus columba*
Raven	*Corvus corax*
Sandhill Crane	*Grus canadensis*
Steller's Eider	*Polysticta stelleri*
Tufted Puffin	*Lunda cirrhata*
Trumpeter Swan	*Olor columbianus*
Willow Ptarmigan	*Lagopus lagopus*

[1]R. Stimmelmayr pers. commun. 1993.

Chapter 3

1991-1992 Winter Mortality of Reindeer on Hagemeister Island

Reindeer living in predator-free environments show an interspecific competition for winter food supplies and in turn this regulates animal numbers (Leader-Williams 1980; Skogland 1985b, 1990). Competition for food affects animal growth and body weight and thereby reproduction and survival (Skogland 1985b, 1990). With an increase in population density, density-independent factors such as severe weather can exacerbate periods of food shortage (Skogland 1985). Catastrophic mortalities during winter have occurred in several insular *Rangifer* populations, for example, barren ground caribou (*R.t.groenlandicus*) on Coats Island (Gates et al. 1986), Peary caribou (*R.t.pearyi)* on the western Queen Elizabeth Islands (Miller et al. 1977), and in reindeer (*R.tarandus*) on Nunivak, St. Matthew, St. Lawrence and the Pribilof Islands (Klein 1968; Scheffer 1951; Swanson and Barker 1991). High population densities in combination with restricted access to winter lichen as a result of adverse snow and ice conditions and/or over-grazed lichen range have been implicated as causes of these winter die-offs.

A total of 144 reindeer were introduced to Hagemeister Island in 1965 and 1967[1]. Management of the herd has been by Native reindeer herders from the village of Togiak. The Hagemeister Island reindeer herd increased in size to approximately a 1,000 head by 1971 and then the population fluctuated from an estimated 590 to 953 animals. Range on Hagemeister Island, in particular lichen vegetation sites, had received heavy use and reduction of the herd to about 450 animals was recommended[2]. By 1990, the herd reached an all-time high of an estimated 1,530 animals. During the late

[1]Grazing permit by BLM (in BLM and US-F&WS files).

[2] 1973 letter by J. Merrick to Messrs. Bavilla, Christian, Gosuk.(in BLM and US-F&WS files).

winter 1991-1992, a die-off of approximately 300 reindeer occurred on Hagemeister Island (J. Gosuk pers. commun.1992). The primary purpose of this study was to investigate the die-off of Hagemeister Island reindeer and to determine the underlying cause of the die-off.

Methods

Weather records were not available for Hagemeister Island. Description of study site and climate are in Chapter 2. All surveys of Hagemeister Island reindeer have been conducted by personnel of US-F&WS Alaska Maritime National Wildlife Refuge. A systematic census was conducted on May 4, 1992 following a report of many dead reindeer on the island (J. Gosuk pers. commun. 1992; Van Daele 1992). Other aerial censuses were conducted on June 5 and 11, 1992. A fixed-wing Supercub PA 18 aircraft was used for all surveys. A standard transect technique as described by Gasaway et al. (1985) was employed. Transects were spaced at 1/2 to 3/4 km intervals. The aircraft was flown at approximately 120 m above ground level. Areas where high winds and turbulence prevailed were flown at higher altitudes of 300-460 m. Reindeer were counted along 0.4 km strips on each side of the aircraft by pilot and observer in the rear seat. Contour flying was used in the mountainous area. On May 4, June 5, and June 11 approximately 75%, 60%, and 100% of the island was sampled, respectively. Reindeer were recorded as adults (> 1 yr. old) or calves. Live animal condition was assessed and recorded based on body contour lines, antler size, and animal movement. Dead reindeer were also recorded along the transects. A composition survey was conducted on June 11, 1992. Reindeer were classified as cows (> 1 yr. old), males (> 1 yr. old), and calves (< 1 yr. old). Post-mortem examinations were conducted on 54 reindeer carcasses from June 5-8, 1992. Age, sex, and location of skeletal remains

were recorded on a topographical map (1:63,000). Reindeer carcasses were classified into 7 age groups on the basis of eruption and wear patterns of lower incisors (Palmer 1934; Miller 1974; Skjenneberg and Slagsvold 1968) (Table 3.1). Sex determination was based on presence or absence of male genitals and antlers.

Six reindeer were shot by the US-F&WS. Body condition was assessed using a field technique as described by Kistner et al. (1980). Complete necropsies were done following standard necropsy procedure (Jones and Hunt 1972). Tissues collected for histopathology were placed in 10% neutral buffered formalin. Fecal samples collected for parasitological examination were chilled at the field camp and subsequently frozen. All formalin-fixed and frozen samples were subsequently examined at the University of Alaska, Fairbanks. Formalin-fixed tissues were trimmed and processed by routine paraffin technique and sectioned. Sections were stained with hematoxylin and eosin for light microscopic examination. Fecal samples were examined using a modified McMaster technique (Sloss 1970). Fat content of bone marrow in mid-femur was determined from a sample of marrow taken from the central portion of the femur and weighed. These were then air-dried until sample weights varied no more than a few mg on succeeding days. The non-fat-soluble residue was not determined (Neiland 1970).

Results

A census on May 5, 1992 determined that there were 497 live reindeer (including 5 calves) and an estimated 163 carcasses on Hagemeister Island. Live animal condition was estimated as poor (visible backbones and tended to stumble as they moved) (Van Daele 1992). On June 11, 1992, there were an estimated 734 live adult reindeer, 200 calves, and 276 carcasses. Live animal condition was estimated as fair

to good condition (no visible backbones and swift movements). Growth of antlers had resumed and the majority of animals had small to medium sized velvet antlers. Shedding of winter coats was not completed. On the basis of the 1990 aerial census count, mortality was calculated to have been about 18% over the winter period. From the May and June, 1992 aerial surveys, peak calving time probably occurred between mid-May and early June.

Fifty-four carcasses were examined from June 5-8, 1992 to determine cause of death. The age distribution of these animals is shown in Table 3.2. Fifty-one of these carcasses were males. The carcasses were located on the northeastern portion of Hagemeister Island and were grouped tightly. Average distance between carcasses was 150 m. The majority (> 80%) of carcasses were found in a curled prone position. The remainder were bedded in a lateral position with legs extended. The immediate area around the carcasses was severely trampled and evidence of cratering was apparent. Antlers were absent in all but 10 animals. The carcasses were severely decomposed and scavenged. Hides were partially present on the head, neck, abdomen, and lower part of the limbs. Lesions from warble fly larvae (*Oedomagena tarandi*) were found on the hide of several carcasses. When present, the hair coat was thick, white in color, and complete. Subjective assessment of bone mineral content (rib breaking) showed no evidence that a deficiency was present. A healed rib fracture was observed in one animal. The femoral bone cavity consistently contained a dried red paper-thin serosal sheet, indicating that little or no fat was present at time of death. A small amount of wet, reddish gelatinous bone marrow filling about 10% of the femoral bone cavity was present in three carcasses.

Body condition of sacrificed adult reindeer (2 females and 4 males) was assessed as fair. This indicated that

animals had responded to the spring green-up. One female was pregnant with a fetus developed to full term. Moderate amounts of internal and subcutaneous body fat stores were present. Femur marrow cores were solid, filling 100% of the cavity. Dry weight fat content ranged from 87.5% to 97.3%. Warble fly larvae and nasal bot flies (*Cephenomyia trompe*) were present in all shot animals. Infestation levels varied from 100 to 150 for warble fly larvae and from 10 to 30 for nasal bot flies. Coccidia oocysts were observed in fecal samples, ranging from 50 to 750 eggs/g feces. *Sarcocystes* spp. were found in the myocardium of 4 animals. No other pathological findings were observed.

Discussion

On the basis of sex and age distribution of examined carcasses, predominantly adult males died during the winter of 1991-1992. The tight concentration of carcasses as well as the range condition in the area of the die-off area suggests that severe weather conditions may have restricted animal movement and restricted access to available forage. The die-off presumably occurred around mid to late winter (December-March) as indicated by the absence of antlers on examined carcasses. The complete lack of bone marrow suggests starvation as cause of death. These results suggest that the over-winter mortality of Hagemeister Island reindeer may reflect a population adjustment to both climatic and overall poor winter lichen range conditions. A pronounced adult male mortality under conditions of food shortage such as over-grazed winter range has been previously demonstrated in reindeer (Klein 1968; Leader-Williams 1980; Reimers 1977), red deer (*Cervus elaphus*) (Clutton-Brock et al. 1982), and musk oxen (*Ovibos moschatus*) (Gunn et al. 1989).

Several studies have shown that reindeer living in over-

grazed or lichen-free areas utilize other forage plants during winter, for example, reindeer on South Georgia Island (Leader-Williams 1988), Svalbard (Reimers 1977), and Umnak Islands (Finstad and Renecker 1991). This suggests that reindeer are more adaptive feeders than previously thought. If reindeer on Hagemeister Island do not depend entirely on lichen during winter, what could have facilitated the predominantly male die-off? A possible answer may be found in the late breeding season of this herd. Results of May and June, 1992 composition counts indicated that females of the Hagemeister Island herd apparently conceived during October versus early September as observed for reindeer herds on the Seward Peninsula. This was confirmed by fetal analysis (see Chapter 4). Male reindeer exhibit a marked rut-associated hypophagia. This results in a dramatic loss of body condition and most of their fat reserves are depleted by the end of rut (Leader-Williams and Ricketts 1982; Tyler 1987; Tyler and Blix 1990). Under this circumstance, periods of food shortage as a result of adverse snow and ice conditions, result in increased mortality of adult bulls from malnutrition (Klein 1968; Leader-Williams 1980; Reimers 1982). A dramatic loss of body condition after icing has been reported for barren-ground caribou on Coats Island (Gates et al. 1986), for Peary caribou on western Queen Elizabeth Islands (Miller et al. 1977), and reindeer on Nunivak Island (T. Tomany-Renecker pers. commun. 1994). There is no conclusive evidence that icing occurred during winter 1991-1992, however, snowfall in Dillingham (M. Hinkes pers. commun. 1992) was greater than in other years. Thus extreme snowfall and/or icing conditions in late winter and poor post rut condition of adult bulls may have precipitated the 1991-1992 winter mortality on Hagemeister Island.

Table 3.1. Classification of age on the basis of eruption and wear pattern of incisor teeth in reindeer[1].

Age (month)	Comment
4-7	deciduous[2] incisors
8-12	incisor 1 permanent
16	all permanent incisors present; no wear
28	incisor 1 shows slight wear
40	incisor 2 shows slight wear
52	all incisors show slight wear
72	canine shows wear

[1]Source: Skjenneberg and Slagsvold 1968

[2]deciduous = milk teeth

Table 3.2. Age distribution of examined reindeer carcasses (n=54)[1] on Hagemeister Island, June, 1992.

Age (months)	Number of Animals
4-7	2
8-12	9
16	20
28	3
40	5
72	11

[1]in four animals age could not be determined.

Chapter 4
The Reproductive Characteristics of Reindeer on Hagemeister Island

The reproductive biology of *Rangifer* is characteristic of a seasonally polyestrus species, with a high reproductive synchrony. Reindeer and caribou can be classified as short-day breeders and mating takes place during autumn, with reindeer breeding approximately 4-6 weeks earlier than caribou (Skoog 1968). Variation in time of breeding season between different reindeer populations has been attributed to differences in nutritional resource availability (Epsmark 1980; Reimers 1982; Reimers et al. 1983c; Skogland 1985b). Under conditions of food shortage, individuals compete for access to preferred, quality forage (Klein 1968; Leader-Williams 1988; Skogland 1985b). Competition will adversely affect growth, fat accumulation, and ultimately reproduction and/or survival (Skogland 1985b). Delays in sexual maturity, (Leader-Williams and Rosser 1983; Skogland 1986) onset of estrus, and/or lengthening of gestation period (Epsmark 1980; Skogland 1985b, 1990), low fecundity rates (Dauphine 1976; Reimers 1983; White 1983), and increased calving intervals (Reimers 1983; Thomas 1982) have been cited as direct effects of food limitation on reproductive performance in *Rangifer*.

During the winter of 1991-1992, a die-off of several hundred reindeer occurred on Hagemeister Island. A field investigation recorded a 2-3 week delay in peak calving time. This was based on aerial surveys of cows and calves in May versus June (Stimmelmayr and Renecker 1992 and 1993). Peak calving time on Hagemeister Island probably was mid-May to early June (see Chapter 3) versus late April to early May for populations of reindeer on the Seward Peninsula, Alaska

(Chetkiewicz 1993). Reindeer were introduced to Hagemeister Island in both 1965 and 1967. The seed animals (124 females and 20 bulls) originated from the woodland caribou (*R.t.caribou*) and reindeer (*Rangifer tarandus*) cross herd on Nunivak Island, Alaska. This herd was established in the early 1920's as a U.S Department of Agriculture (USDA) cross-breeding experiment (Stern et al. 1980). Swanson and LaPlant (1987) concluded that poor winter lichen range condition on Hagemeister Island had facilitated the 1991-1992 die-off. If the reindeer population on Hagemeister Island was indeed limited by winter lichen range than the shift in calving time would be an effect of density-dependent food limitation and not be linked to their breeding history. To test the hypothesis whether food resources are limited on Hagemeister Island the reproductive performance of female reindeer was investigated. The main objectives of this study were to determine: (1) the time of the breeding season of Hagemeister Island reindeer; (2) to quantify reproductive parameters as indicators of herd performance; and (3) to explore the underlying cause such as genetics and/or effects of density-dependent food limitation on reproductive performance of the observed shift in calving season.

Methods

Reproductive Analysis

A total of 67 reproductive tracts were collected from female reindeer shot by US-F&WS during the 1992 and 1993 extirpation of reindeer from Hagemeister Island. Body condition of shot females was assessed using Kistner's scoring technique (Kistner et al. 1980). Lactational status of shot and air-lifted live females was determined by visual inspection and palpation of the udder. Animals ≤ 5 years old

were aged to the nearest year on basis of eruption of incisor teeth and teeth wear patterns (Miller 1974; Skjenneberg and Slagsvold 1968; Palmer 1934). As animals get a year older in May (calving season) half a year were added to each animal's age. Animals > 5 years were classified as 5^{+} years old. Uteri and ovaries were removed within 2 h after death, individually bagged, and either allowed to freeze at ambient temperature (November 1992) or preserved in 10% formalin solution (September 1993). Frozen specimens were subsequently stored at -20° C until they were examined. The analysis of reproductive organs consisted of several steps.

1. Pregnancy or non-pregnancy was assessed from presence or absence of embryonic or fetal tissues in the open-slit uterus.

2. Fetuses were removed, weighed, sexed, and fetal crown-rump length was recorded using Vernier Calipers (precision of 1 mm), but caution was taken not to stretch the fetuses.

3. On the basis of external characteristics, fetuses were classified as tailbud embryos, late embryos, or early fetuses. Fetuses within the early fetus stage were further subdivided according to stage of eyelid development, crown-rump length, and differentiation of external genitalia. External characteristics of the different fetal developmental stages are summarized in Table 4.1.

4. Caruncles in each horn were counted and their length, width, and height recorded. Total caruncle area per horn was calculated using the following equation: area = length * width * Pi / 4.

5. Ovaries of complete pairs were sliced sagitally into 1 mm sections joined at their hilal edges (Cheatum 1949; Golley 1957). Sections were back lighted and examined macroscopically for functional and regressed (pigmented) luteal structures and follicles. The luteal structures were classified in 6 categories, primary corpus luteum (PCL) corpus luteum hemorrhagicum (CLH), corpus luteum spurium (CLS), corpus luteum verum (CLV), corpus luteum of post conception (CLPC), corpus luteum accessorium (CLA), corpus rubrum (CR) and corpus albicans (CA) (Langvatn 1992). Morphological and functional characteristics of these luteal structures are summarized in Table 4.2. With a Vernier caliper, the maximum and minimum diameters across the largest exposed face of each structure were measured and the two diameters averaged. Follicles were tallied in two diameter classes: > 2 and ≤ 5, and > 5 and < 10 millimeter.

Each step in the analysis was performed without reference to data on age, lactational status and body condition for a particular animal. In the various sections of this investigation, only parts of the total reproductive material (n=67) were suitable for the respective analyses due to loss of tissue, damaged tracts, different methods of preservation, reproductive status, and sample size constraints. For this reason, numbers for the different analyses varied.

Animal Behavior

Observations of herd organization such as group composition and size, distribution of the herd on the island, and reproductive behavior (i.e. sparring; scent-marking; breeding) of the herd were made in November, 1992 and August-October, 1993.

Statistical Analysis

The frequency of occurrence of CLPC was tested by Chi-square test (Zar 1984). Production of ova within pair of ovaries were compared by a paired-sample *t* test (Zar 1984). Least squares regression analysis was used to compute fitted linear models for data on luteal scars in 1-4 year old female reindeer (Zar 1984). The level of significance was $P < 0.05$.

Results

Animal Behavior

By early August, 1993, mature bulls on Hagemeister Island had begun to show preparatory features for the rut as indicated by hypertrophy of neck muscles and hind leg urine spraying. By September 3, mating groups consisted of loosely organized harems. The majority of bulls had shed their velvet and displayed rutting behavior such as tending of females, sparring and breeding. However, velvet was not shed from the antlers of most cows. Approximately 25-30 individual herds, ranging in size from 10-70 animals were widely dispersed across the island. By November 1992, reindeer on Hagemeister Island were sexually segregated (post rutting season) and moved in large cow/calf aggregations with yearlings, and smaller bands of young and adult bulls. All animals had hard antlers and some older bulls had already shed their antlers.

Reproductive Analysis

Body Condition

All females shot in November, 1992 were in excellent body condition. Internal body fat stores (greater omentum, heartbase and coronary groove, pericardial sac, and perirenal kidney area) were estimated at a 100%. Due to

logistics, ratings of subcutaneous fat sites could not be obtained. However, based on the symmetrical appearance of carcasses, and absence of skeletal prominences such as hip bones, backbones, and ribs it was concluded that animals were in an overall good body condition. With the exception of one animal, females shot in September 1993 were in good to excellent body condition. The age distribution of females collected in 1992 and 1993 is summarized in Table 4.3.

Lactational Status

In 1992, none of the shot (n=48) and airlifted live female reindeer (n=30) on Hagemeister Island were lactating. In 1993, nine of the 19 shot adult females were lactating. Results for airlifted live yearling and adult female reindeer in 1993 are summarized in Table 4.4.

Luteal Activity

In 1992, sampling was consciously biased towards pregnant female reindeer to obtain sufficient fetal material. Samples with complete pairs of ovaries from females > 1 year old (n=38) were included in the analyses. The CLV was always ipsilateral to the uterine horn occupied by the fetus, thus indicating no fetal transmigration. The CLV occurred 14 times on the right and 24 times on the left side. The ratio of the CLV did not differ significantly using a chi-square test. The ovaries of these 38 females had produced 183 corpora lutea (the total of all luteal structures), 98 right, 85 left. The ratio of all corpora lutea did not differ significantly using a chi-square test. A proportion (46.2%) of females had one ovary which dominated in the production of ova ($P < 0.001$). CLPC were distinguished from CLV by their smaller diameter. Average diameter (cm) and SD of CLPC was 0.43 +/- 0.11 cm versus

1.39 +/- 0.18 cm for CLV. Five of 38 females had one CLPC. The distribution was 2 contralateral and 3 ipsilateral. The difference between CLPC occurrence in females for age class 1 (1-2 years old) and 2 (> 3 years old) was not significant as determined by a chi-square test.

No luteal scars were found in calves (n=2) born in 1992. However, luteal scars were found in 5 (62.5 %) of 8 females (1 year old age class). The regression of luteal scars (**y**) on age (**x**) of females 1.5 - 4.5 years old was significant (r^2 = 0.35; SEb = 0.9884; P < 0.01); **y = 0.476 + 0.540x**) (Fig.4.1a).

In 1993, no fetal structures were observed and caruncles were inconspicuous. Luteal structures observed were classified as CLP, CLH, or CLS. Seventeen (89.5%) of 19 females had a functional CLP. Eight of these were CLH. Three (17.6%) of the 17 females had one CLS and one female had two CLS. No luteal scars were found in 1.5 year old females (n=2). The regression of luteal scars (**y**), on age (**x**) of females 1.5 - 4.5 years was significant (r^2 = 0.56; SEb = 1.37; P < 0.01; **y = -0.858 + 1.26x**) (Fig.4.1b).

Follicular Activity

In 1992 (n=38), 2 females had follicles in the > 5 < 10 mm diameter class and 12 had follicles in the > 2 <5 millimeter class. In 1993 (n=19), the distribution was 9 and 10, respectively.

Reproductive Pathology

No pathological conditions were observed in material collected in 1993 (n=19). However, in 1992 reproductive disorders were detected in 11 (23.37%) of 46 animals. Five animals had single paraovarian cysts. Three animals had mild

a endometritis which included one animal that did not have a CLV despite the presence of a well-developed fetus. Multiple endometrial cysts were found in 3 animals.

Development of Fetus

Clear signs of attachment of the placenta were observed in all females with the exception of two fetuses (tailbud embryo). The allantochorion extended into both horns. Thirty-three females had 6 caruncles (3 caruncles per horn). Twelve animals had caruncle counts below (3-5) and 15 had counts above (7-8). Caruncles in the horn opposite to the one containing the fetus were significantly (both $P < 0.001$) smaller in size. One (2.22%) in 45 animals had twins. Both fetuses were classified as early fetuses. Twenty-seven (64.3%) of 42 fetuses had a crown-rump length (CRL) < 5 cm (range of 3.0 to 4.95 cm). These fetuses were excluded from the sex ratio analysis because determination of sex by macroscopic examination of the genitalia is only accurate when the fetus has reached a length of 5 cm (Roine 1974). Of the 9 fetus with a CRL > 5 cm, 7 were male and 2 were female. The sex ratio did not differ significantly as determined by a chi-square test.

Two (4.76%) of 42 fetuses were tailbud embryos, while the remainder (95.24%) were classified as early fetuses. Within this group, individual fetal development differed with respect to eyelid formation and differentiation of external genitals (Table 4.5). The CRL measurements of Hagemeister Island fetuses varied between 0.9 and 8.1 cm. The average CRL for females 1-2 years and > 2 years was 4.55 +/- 1.38 cm and 4.54 +/- 1.3 cm, respectively. There was no significant difference in CRL measurements of fetuses conceived by 1-2 year old females (n=15) and by females > 2 years old (n=27). Backward stepwise regression of CRL (**y**) on developmental

stage (**x1**), age of hind (**x2**), sex of fetus (**x3**), and fetal weight (**x4**) concluded that the best regression model was **y = 2.72 + 0.356x1 + 0.142 x4** (r^2 = 0.85; SE_b = 0.55; P < 0.01).

Fetal weight (FW) measurements varied between 0.1 and 31.2 g. The average FW for 1-2 year and > 2 year old females was 6.88 +/- 4.02 g and 7.1 +/- 6.5 g, respectively. There was no significant difference between FW of fetuses conceived by 1-2 year (n=15) and > 2 year old females (n=27). Backward stepwise regression of FW (**y**) on developmental stage (**x1**), age of hind (**x2**), sex of fetus (**x3**), and CRL (**x4**) concluded that the best regression model was **y = -9.70 + 3.68 x4** (r^2 = 0.77; SE_b = 2.68; P < 0.01). On the basis of comparative data from reindeer (Roine 1974) (Table 4.6), > 80% of the fetuses were estimated to be about 7 weeks old (Table 4.7).

Discussion

Timing of Conception

The results of fetal analyses indicated that in 1992, > 80% of pregnant females on Hagemeister Island conceived between October 6 and 10. Approximately 10% of the embryos examined were conceived before this period, possibly about October 1. Only two fetuses (estimated 5 weeks old) were conceived after October 10. This indicated that the end of the mating season was possibly about the 3rd week of October. These data suggested that the mating season was approximately a month in duration with the peak period of conception during the first two weeks. This hypothesis is supported by behavioral observations such as timing of velvet shedding, breeding, lactational status of females in early winter (1992) versus early autumn (1993), and by the analysis of the ovarian material collected during September, 1993. On the basis of follicular activity, the majority of

females appeared to be in proestrus during September. However, the majority of females had regressing (CLS) or functional corpora lutea of the current year (CLP or CLH) which indicated that one estrus cycle had occurred. It is unclear whether this indicated conception failure in these females or occurrence of "silent heat", which has been reported in caribou, but not in reindeer (Leader-Williams and Rosser 1983; McEwan and Whitehead 1980; Bergerud 1975). The Hagemeister Island breeding season in comparison to other Alaskan *Rangifer* populations is more similar to caribou in central and southern Alaska than reindeer on the Seward Peninsula, Alaska. The main period of the rut for caribou in these regions takes place between September 28 and October 15, with the peak probably occurring about October 6 (Skoog 1968). The breeding season on the Seward Peninsula, Alaska takes place from late August until mid-September (Dieterich and Luick 1971).

Productivity

Regressions of luteal scars on age were significant ($P < 0.05$) for both years. However, for the 1992 data only 35% of the total variation could be explained by the regression between the two parameters, in contrast to 56% for the 1993 data. Caution seems warranted when interpreting this regression equation. The large overcount of scars in females 1 year old appears to be responsible for the poor fit of the regression model. The presence of luteal scars suggests that calves born in 1991 attained physiological puberty. In 1993, an insufficient sample size of reproductive tracts of 1 year old females (n=2) precluded the testing of this hypothesis. However, 9 out of 35 yearlings (25.7%) airlifted from Hagemeister Island to the mainland during September, 1993 were lactating (Table 4.4). This indicated that these

yearlings had conceived as calves. Under excellent summer range conditions, this has been reported by Hadwen and Palmer (1922) for Alaskan and by Ropstad et al. (1991) for Norwegian reindeer, but not for caribou (Dauphine 1978; McEwan 1963; Skoog 1968). Yearlings in this study had luteal scar counts that ranged from 1-10, which exceeded that expected for their age class. High numbers of luteal scars could be caused by recurring cycles, high occurrence of CLPC, or luteinizing unruptured follicle syndrome (LUF). For the Hagemeister Island population, recurring cycles can not be excluded. Multiple ovulations being the cause, however, seems unlikely. CLPC have a lower frequency of occurrence in the Hagemeister Island population than previously reported for reindeer on South Georgia Island (79%) (Leader-Williams and Rosser 1983), for the Kaminuriak population of barren-ground caribou in Northern Canada (35.2%)(Dauphine 1978). However, Skoog (1968) reported only 18% for Alaskan caribou. The number of follicles ovulating per cycle tends to be species-specific and ranges between 1-3 in *Rangifer* (McEwan 1963; Roine 1974). Differences in ovulation rate between reindeer and caribou is likely due to genetics (Leader-Williams and Rosser 1983), however, the influence of nutrition or stress cannot be excluded (Rivier and Rivest 1991).

The observed twinning rate of 2.2% in the Hagemeister Island population is in agreement with previously reported studies with reindeer (McEwan 1971; Palmer 1934; Roine 1974). The general low frequency of twins in *Rangifer* populations, despite multiple ovulations, suggests the existence of a mechanism which prevents the successful implantation of two conceptuses. It has been postulated that single births are a selective adaptation for the nomadic and social habits of this species (McEwan 1964).

LUF has been reported to occur in caribou, however, the respective studies conflict with respect to how common LUF is (Dauphine, 1978; McEwan 1963; Skoog, 1968). LUF is an ovulatory disorder that is characterized by a failure to eject an oocyte, or in some cases the ovulation of inherently deficient and therefore unfertilized eggs (Johnson and Everitt 1991). In human reproduction, this condition has frequently been associated with stress. Failure of ovulation is possible due to the observed stress-related immediate decrease in LH secretion (Rivier and Rivest 1991). For ovulation to occur, a surge of LH is required during the pre-ovulatory phase (Johnson and Everitt 1991).

The pregnancy rate of 1.26 in 1993 (= the slope of the regression of luteal scars on age) for Hagemeister Island reindeer indicates a higher productivity than previously reported for other *Rangifer* populations (Fig.4.1b). For example, 0.93 for reindeer on South Georgia Island (Leader-Williams and Rosser 1983) and 0.84 for the Kaminuriak barren-ground caribou in Northern Canada (Dauphine 1978). The low estimation of lactating females in 1993 (Table 4.4) suggests only an estimated pregnancy rate of 52.5% for 1992. Udder distension has been used as an indicator of parturition in free-ranging North American caribou populations (Bergerud 1964; Skoog 1968) and reindeer on the Seward Peninsula, Alaska (Dieterich 1986; Renecker and Chetkiewicz 1993). However, the involution of the mammary gland in *Rangifer* after calf loss or after weaning is rapid. Thus, the technique is only considered to be reasonably reliable if surveys are conducted at the end of the peak calving period (Whitten 1989). The timing of the survey on Hagemeister Island rules out the use of this technique as an accurate method for estimating calving rates. However, it

can serve as an indicator for the timing of weaning. On the basis of lactational status of female reindeer on Hagemeister Island in 1992 and 1993, weaning appeared to take place between mid-October and November. These results are comparable with the Porcupine Caribou Herd in northeastern Alaska (K. Gerhart pers. commun. 1994). Weaning for the Porcupine herd begins after the rut (October) and the majority of females are dry by the end of November (K. Gerhart pers. commun. 1994).

The reproductive physiology of reindeer on Hagemeister Island reflects a cycle that is indicative of a caribou x reindeer cross population as would since the breeding history is known. Preliminary results of molecular genetic analysis of tissue material from this herd also support this conclusion (M. Cronin pers.commun. 1994). The reproductive biology of the population shares traits of both reindeer and caribou. If nutritional stress is indeed associated with decreased reproductive performance via reduced ovulations then there is no evidence that the herd experienced nutritional stress in 1991 or 1992. However, this conclusion does not dismiss that the Hagemeister Island population was at a high population density (Chapter 6).

There is no clear explanation for the higher luteal scar counts in 1-year old female reindeer on Hagemeister Island. However, similar findings have been reported previously for two other reindeer populations, both at high population densities, namely the St. Matthew Island reindeer herd (Klein 1968) and Busen herd on South Georgia Island (Leader-Williams and Rosser 1983). In small mammals, high population density has been associated with suppression of reproductive functions (Lee and McDonald 1985). The nature and intensity of these responses appear to differ between species and

sexes, and are related to the age and social status of the individual. Complete inhibition of reproductive function has been shown in subordinate and younger animals, but not in dominant individuals. If the high frequency of luteal structures in calves on Hagemeister, South Georgia, and possibly St. Matthew Islands is indeed associated with the high population density of the respective herds then this would be the first evidence for an effect of high density on reproductive function in large herbivores.

Table 4.1. Classification of external characteristics of different fetal developmental stages for reindeer embryos[1,2].

Stage	External Characteristics
Tailbud Embryo (TE)	Embryo C-shaped; fourth branchial arch present; fore and hind limb bud present; optic cup well formed; eyes pigmented.
Late Embryo (LE)	grooves between forelimb and hindlimb digits; genital tubercle present; pinna partly covers acoustic meatus.
Early Fetus	digits clearly separated; pinna covers acoustic meatus; tongue visible and palate fused.
EF1	eyelids not present.
EF2	eyelids forming.
EF3	eyelids fused and <5 cm CRL.
EF4	eyelids fused, >5cm CRL, and external genitals differentiated.
EF5	same as EF4, but >6 cm CRL.

[1]Source: Evans and Sack 1973

[2]Source: Roine 1974

Table 4.2. Morphology and functional characteristics of corpora lutea in red deer *Cervus elaphus*)[1].

Structure	Definition
PCL	develops from an ovulated graafian follicle; it is not associated with a conceptus; by definition it can turn into a CLS or CLV, depending on non-conception or conception. Mean diameter: 4-10 mm. Color: pale yellow.
CLH	recent PCL where central cavity is filled with blood.
CLS	regressing PCL as a result of failed conception. Mean diameter: 2-8 mm. Color: same as PCL.
CLV	luteal structure functionally related to a conceptus; Mean diameter: 7-16 mm. Color: same as PCL.
CLA	luteinized, non ruptured follicle (LUF); Mean diameter: 2-5 mm. Color: same as PCL.
CLPC	recent luteal structure occurring in the same pair of ovaries as a CLV. Mean average: 5-10 mm. Color: same as PCL.

Table 4.2., page 2

Structure	Definition
CR	regressing luteal structure less than 12 months old derived from a CLV. Mean diameter: 3-6 mm. Color: bright orange to reddish brown.
CA	represent further regression stages of CR. Mean diameter: < 2mm. Color: pale grey or brown.

[1]Source: Langvatn 1992

Table 4.3. Estimated ages of female reindeer collected in November, 1992 and September, 1993 on Hagemeister Island, Alaska.

	Number of Reindeer	
Age (year)	1992	1993
0.5	2	0
1.5	10	2
2.5	8	5
3.5	2	1
4.5	9	5
≥ 5.5	17	6
Total	48	19

Table 4.4. Lactational status of live airlifted female reindeer from Hagemeister Island to the mainland during 1993.

	Number of Animals		
Age Class	Lactating	Non-Lactating	Total
Yearlings	9	26	35
Adults	53	48	101

Table 4.5. Relative frequency of fetal developmental stage in fetuses sampled from reindeer on Hagemeister Island in 1992.

Class	Percentage
Tailbud embryo	4.8
Early Fetus 1	35.7
" " 2	19.1
" " 3	11.1
" " 4	19.1
" " 5	9.5

Table 4.6. Crown-rump length and fetal weight of fetuses taken from Finnish reindeer[1]. Data are presented as mean (+/-SD). Sample sizes are given.

Age (weeks)	Sample size	Crown-Rump-Length (cm)	Sample size	Fetal Weight (g)
4	13	0.65(0.16)		
5	21	1.1(0.37)		
6	19	2.28(0.58)		
8	7	6.83(1.15)	34	13.3(7.7)
9	34	7.87(1.23)	32	20.9(8.5)
10	32	8.23(1.24)	10	24.8(9.6)
12	10	13.37(1.92)		

[1]Source: Roine 1974

Table 4.7. The age distribution of fetuses (n=42) collected from female reindeer on Hagemeister Island in 1992.

Age (weeks)	No. of conceptions	%
5	2	4.8
7	35	83.3
8	4	9.5
9	1	1.9

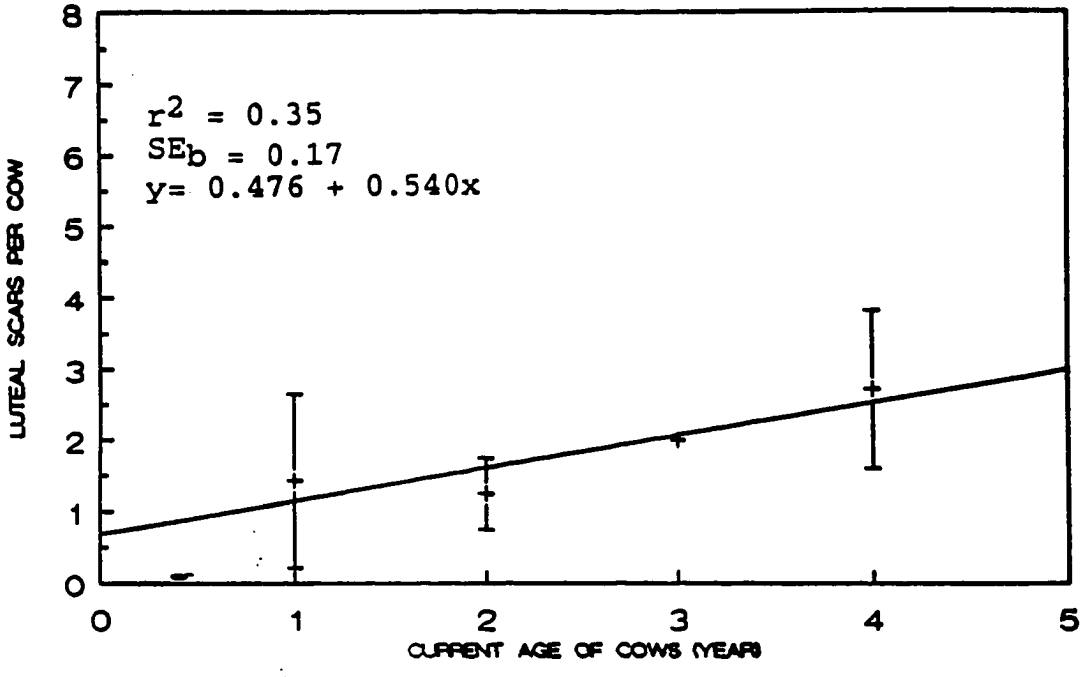

Fig.4.1a. Regression of the number of luteal scars (mean +/- SD are shown as solid bar) on the age of twenty 1-4 year old reindeer on Hagemeister Island in 1992.

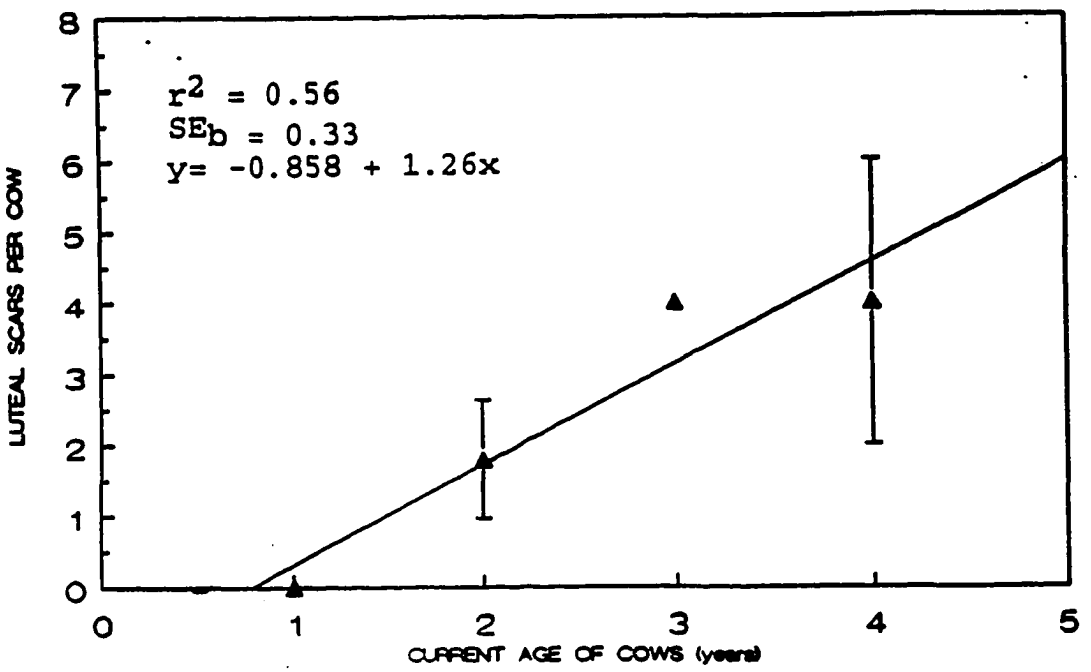

Fig.4.1b. Regression of the number of luteal scars (mean +/- SD are shown as solid bar) on the age of thirteen 1-4 year old reindeer on Hagemeister Island in 1992.

Chapter 5
Body Condition and Weight of Reindeer on Hagemeister Island

It is a widely accepted hypothesis that the abundance of large mammals is regulated by extrinsic factors such as food supply, predation, or both (Bergerud 1980; Caughley 1970; Messier 1989; Skogland 1985a). For predator-free closed populations such as insular or fenced, regulation is manifested through direct effects of food shortage upon demographic rates, which determine rate of population increase. Under conditions of food shortage, intraspecific competition occurs for access to preferred, quality forage. This competition will adversely affect growth, fat accumulation, and ultimately, reproduction and/or animal survival (Caughley 1970; Skogland 1985b). Effects of density-dependent resource limitation on body size and recruitment rate have been demonstrated in reindeer on St. Matthew (Klein 1968), reindeer in Norway (Skogland 1983, 1986, 1990; Reimers 1983); and caribou in Alaska (Valkenburg et al. 1989). Reindeer were introduced to Hagemeister Island, in 1965 and 1967[1]. On the basis of initial carrying capacity, it was concluded that the range on Hagemeister Island could support approximately a 1,000 animals. In the absence of large predators, the herd increased to an estimated 1,011 animals by 1971 (see Chapter 6). Concerns of over-grazing were expressed and reduction of herd size to 450 animals was recommended[2]. Herd reduction proved to be difficult and it continued to fluctuate between 500 and 800 animals. A range survey in 1987 confirmed that winter range conditions, in particular lichen producing sites, had digressed and were severely over-grazed (Swanson and LaPlant

[1] Grazing permit by BLM (in BLM and US-F&WS files).
[2] 1973 letter by J. Merrick to Messrs. Bavilla, Christian, and Gosuk (in BLM and US-F&WS files).

1987). By 1990, the herd reached an all-time high of 1,530 animals, and during the winter of 1991-1992, a die-off occurred (see Chapter 3). This die-off was attributed to poor winter lichen range on Hagemeister Island (Swanson and Barker 1993). The herd performance of the reindeer population on Hagemeister Island was investigated to test the hypothesis that winter lichen range limited this reindeer population. The objective of this study was to explore the relationships between body condition (seasonal cycles of body weight and condition; carcass and organ weights and various physical indices of condition) and food availability. Results are compared to measurements that were recorded for reindeer from the St. Matthew (Klein 1959, 1968) and Nunivak Islands (Klein 1981).

Methods

Five seasonal collections of reindeer were conducted from November 1992 - October 1993 (Table 5.1). A description of measurements recorded is summarized in Table 5.2. Animals were collected typically over a one week period. Body condition was assessed using a field technique as described by Kistner et al. (1980). Complete necropsies were performed following standard necropsy protocol (Jones and Hunt 1972). Tissue samples were chilled at the base camp and subsequently stored at - 20° C until they were examined. Animals ≤ 5 years old were aged on the basis of tooth eruption and wear pattern (Miller 1974; Skjenneberg and Slagsvold 1968). Animals > 5 years old were classified as 5^{+} years old.

Statistical Analysis

Differences between means of measured parameters were compared by analysis of variance (Zar 1984). The level of significance was $P < 0.05$.

Results

Body Weight

In 1992, there was no significant difference between liveweight of either male and female calves or yearlings (Table 5.3). However, there was a significant difference ($P < 0.05$) between mature female and male liveweight (Table 5.4). Adult female reindeer were heavier than male adults.

In 1993, live weights of male and female calves (Table 5.3) and adults (Table 5.4) were significantly different. ($P < 0.05$). Male calves and adults were heavier than female calves and adults, respectively. There was no significant difference between liveweight of male and female yearlings (Table 5.3).

There was no significant difference between liveweights of calves and yearlings collected in 1992 and 1993. However, there was a significant difference ($P < 0.05$) between liveweights of both males and females collected in 1992 and 1993 (Table 5.3).

Carcass Weights and Indices of Condition

No significant seasonal changes were observed in most measured parameters for adult males and females (Table 5.5 and 5.6). As a result body condition indices for each sex were pooled. Carcass weight and gastrochnemius muscle weight varied significantly ($P < 0.05$) between sexes (Table 5.3). August field-dressed weight varied significantly ($P < 0.05$) between sexes (Table 5.3). Sample size for the autumn period precluded statistical analysis.

Fat Reserves

August and September depth of rump fat varied significantly ($P < 0.05$) between sexes (Table 5.3). Kidney fat reserves also varied significantly ($P < 0.001$) between sexes (Table 5.3). Both fat reserves were greater in males than in females.

Internal Organs

Weights of liver and heart were significantly ($P < 0.001$) different between the sexes (Table 5.3). Internal organ weights were greater in males than in females.

Skeletal Size

Total body length and femur length in adults (>2 years) varied significantly ($P < 0.001$) between the sexes (Table 5.3). Skeletal size was greater in males than females. There was no significant difference in mean total body length of yearlings between the sexes (Table 5.4).

Liveweights and skeletal size of adult reindeer on Hagemeister Island were compared to other studies on reindeer and caribou (Tables 5.7-5.8).

Discussion

Sexual Dimorphism

Similar to results from other *Rangifer* populations (Klein 1968 and 1981; Leader-Williams and Ricketts 1982; McEwan and Whitehead 1970; Quellet 1992), there is a pronounced sexual dimorphism in body size, body weight, and organ weight between adult male and female reindeer on Hagemeister Island, but not in yearlings (Tables 5.3 and 5.4). A significant sex difference in body weight appears to be present also in calves during late autumn (September 1993).

However, no sex difference could be detected by a later date (the previous year, November 1992). This could possibly be due to the smaller sample size in 1992.

Seasonality of Body Condition

Reindeer, like other cervids show marked circannual fluctuations in body weight and composition. Fat reserves are deposited in *Rangifer* in the order of bone marrow, followed by kidney fat and then rump fat (Leader-Williams and Ricketts 1982). The depletion of fat reserves is in reverse order. Changes in body weight and fat reserves are preceded by changes in organ weights and gastrointestinal tract weight (Leader-Williams and Ricketts 1982; Quellet 1992; Tyler 1987). There is a clear sex difference in timing of seasonal fluctuations of body condition. Males attain prime condition prior to the rut, whereas females do not attain prime condition until late autumn (Adamczewski et al. 1987b; Leader-Williams and Ricketts 1982; Tyler 1987). Due to small sample size and high data variability, no significant seasonal changes were found for most measured parameters in this study.

The results on kidney fat weight for males suggest that by late spring (May) kidney fat deposition was completed. However, deposition of rump fat continued into late summer (August). For females, results indicate that presumably the energetic demands of lactation severely reduce the ratio of fat deposition as illustrated by the non-significant changes in depth and weight of rump and kidney fat weight. Over 50% of mature females examined on Hagemeister Island were lactating in September (1992), but not in November (1993). The observed period of weaning for the Hagemeister Island herd is comparable to the Porcupine Caribou herd (K. Gerhart pers. commun. 1994). Females from this herd begin weaning

shortly after the rut (September-October) and the majority of females are dry by the end of November (K. Gerhart pers. commun. 1994). The differences between live body weights in 1992 and 1993 further illustrate the clear dimorphism between sexes in regards to time of prime body condition. Males had reached peak body condition prior to the rut (September). Females presumably had attained this level by late autumn (October) and started to loose body condition by early winter (Novemeber). The significant decline in body weight for males after the rut reflects the energetic demands associated with reproductive activity during the breeding season.

In cervids, liver weights have been used as an index of an animals metabolic state. Seasonal variation in liver weight of *Rangifer* have been associated with changes in forage quality (Adamczewski et al. 1987b; Leader-Williams and Ricketts 1981). Results in this study would indicate a prolonged availability of high quality forage on Hagemeister Island extending from May through mid-September. In other studies of high-arctic insular *Rangifer* populations, such as caribou on Coats Island and Southhampton Island, the occurrence of high quality forage and concomitant greater liver weights was restricted to the summer months (Adamczewski et al. 1987b; Quellet 1992). This variation is most likely due to latitudinal and climate difference of the these islands.

Average organ weights for adult females on Hagemeister Island were comparable to those reported by Adamczewski et al. (1987) for adult female caribou collected during summer (June-August) on Coats Island, NWT, Canada. They reported maximum liver weights of 1.8 kg and average heart weight of 0.8 kg. Kidney fat weights for adult females on Hagemeister Island fell within their reported range of 40 g to 90 g for

the summer period. Depth of backfat for Hagemeister females was at the lower end of their reported range of 1 to 2 cm. This suggests that environmental conditions on Hagemeister Island are inferior to those reported for Coats Island. However, several studies on reindeer and caribou have found that caribou have considerably heavier body weights and more stable fat reserves than reindeer (Dauphine 1978; Leader-Williams and Ricketts 1982). Thus extent of fattening in *Rangifer* may be linked to heredity, next to forage quality, lactational status, and insect harassment (Cameron et al. 1993; Reimers et al. 1982; White and Hauer 1989). Results in this study could reflect genetic differences rather than differences in environmental conditions.

Body Weights and Size

Data on liveweights for free-ranging Alaskan reindeer during early winter are not available. However, comparable data during late summer are available for adult reindeer on Nunivak Island and for all age classes from Mackenzie Delta, NWT (Table 5.7). Body weights for reindeer on Hagemeister Island fall within the ranges reported for these herds. Interestingly, liveweights of calves and yearlings between 1992 and 1993 did not differ significantly despite the drastic population reduction, which took place in November 1992 (see Chapter 6). A subsequent increase in birth weight after reduction of the high density Hardangervidda wild reindeer herd in Norway was reported (Skogland 1990).

Measurement of skeletal size has been used in *Rangifer* as an index of habitat quality or density-dependence (Reimers et al. 1983a; Klein 1968; 1970; 1981; Skogland 1990). Average skeletal size of adult reindeer from Hagemeister Island appears to be slightly smaller than animals from Nunivak and St. Matthew Islands (Klein 1968 and 1981) (Table

5.7). The crossbred reindeer population on Nunivak Island provided the seed animals for Hagemeister and St. Matthew Islands (Klein 1959; Stern et al. 1980). This may indicate that habitats and environmental conditions vary between the respective islands. However, the sensitivity of this index has been questioned. For example, Leader-Williams and Ricketts (1982) could not show consistent changes in skeletal size between three herds of reindeer living at different densities on South Georgia Island ranges that differed in quality.

There is a pronounced sex difference in body weight and skeletal size between adult male and female reindeer on Hagemeister Island. Males are significantly heavier and larger than females as would be expected. Seasonal fluctuations in body condition and body weight for males and females differ with respect to reproductive activity. Body condition in adult male reindeer on Hagemeister Island peaked before the rut and in females by late fall (October). Body condition and body size of reindeer on Hagemeister were comparable with reindeer from Nunivak Island (Table 5.8). Thus there is no conclusive evidence that a density-dependent decrement in size of reindeer was present on Hagemeister Island. This suggests that range quality on Hagemeister Island has not been reduced sufficiently for a decrease in body size to have occurred in spite of the size of the herd.

Table 5.1. Numbers of mature females and males, calves, and yearling females and males collected during 1992 and 1993 on Hagemeister Island, Alaska.

		Yearling		Adult	
Collection Period	Calves	Males	Females	Males	Females
May 21-28 1993	-----	-----	-----	4	-----
July 26-3 Aug. 1993	1	-----	-----	2	2
late August-early October 1993	-----	1	-----	2	1
November 1992 late August-early October 1993	14	2	4	33	4
Collection[1]	81	11	28	103	5
Collection[2]	-----	-----	-----	21	34

[1]collection = only live weight. All females in 1992 were non-lactating. In 1993, > 50% of the adult females and > 30% of the yearling females were lactating.

[2]collection = only total body length, liver weight, heart weight, kidney fat weight, and depth of rump fat.

Table 5.2. Measurements taken on live and sacrificied reindeer from Hagemeister Island.

(1) Total body weight	live body weight using Tru-Test livestock scales[1]. Weights were read to the nearest 0.1 kg.
(2a) Field-dressed weight	weight of the animal without internal organs; excretory and reproductive organs removed; kidneys and their fat deposit remained in the carcass. Weights were taken with a 45 kg spring scale[2]. Animals were weighed in segments(for example hind quarters, thorax etc). Weights were read to the nearest 0.250 kg (Langvatn 1977).
(2b) Carcass weight	estimated from equations calibrated for free-ranging Alaskan reindeer (Ringberg et al. 1981).
(3) Liver weight	weights were taken with a 300 (g) spring scale[3]. Weights were read to the nearest g.
(4) Heart weight	weights were taken with a 300 (g) spring scale[3]. Weights were read to the nearest g.
(5a) Kidney weight	weights were taken with a 300 (g) spring scale[3]. Weights were read to the nearest g.
(5b) Kidney fat weight	the combined weight of kidney fat from both sides was calculated by subtracting kidney weight from the weight of the kidneys with attached fat. Weights were taken with a 300 (g) spring scale[3]. Weights were read to the nearest g. (Leader-Williams and Ricketts 1982).

Table 5.2., page 2.

(6)	M.gastrochnemius weight	weights were taken with a 300 (g) spring scale[3]. Weights were read to the nearest g.
(7)	Rump fat depth	the maximum depth of rump fat was measured at the base of the tail. (Langvatn 1977). A flexible steel tape was used. Values were read to the nearest 0.1 cm.
(8)	Total length of animal	from most anterior point of the snout to the base of the tail on the dorsal side (Langvatn 1992). A flexible steel tape was used. Values were read to the nearest 0.1 cm.
(9)	Total length of femur.	from the top of caput femoris to the most distal point of condylus medialis (Langvatn 1992). An osteometric board was used. Values were read to the nearest 1 mm.

[1]Tru-test scales (Model AG500, Tru-test Distributors, 241 Ti Raku Drive, P.O.Box 51-078 Pakarunga, Auckland, New Zealand;

[2]Hanson spring scale (Model 8910, Shubuta, Missouri 39360, USA.

[3]Pesola scales, Made in Switzerland.

Table 5.3. Body condition indices and total body length of calves and yearling reindeer collected in 1992 and 1993 from Hagemeister Island. Data are expressed as mean (+/-SD). If not otherwise indicated year of collection was 1993.

Index	Level of Significance[1,2]	Calves: Males	Calves: Females
Total body weight (kg)			
1992 November	n.s.	48.8 (7.7) (n=5)	47.6 (10.8) (n=9)
1993 September	*	52.8 (7.8) (n=45)	48.9 (9.0) (n=36)
		Yearlings	
		Males	**Females**
Total body weight (kg)			
1992 November	n.s.	77.0 (21.92) (n=2)	72.00 (9.1) (n=4)
1993 September	n.s.	72.1 (10.9) (n=11)	75.8 (9.7) (n=28)
Total body length (cm)	n.s.	165.1 (9.6) (n=9)	159.5 (0.7) (n=2)

[1] n.s. = values in the same row are not significantly different at the 5% significant level. [2] * = values in the same row are significantly different ($P < 0.05$).

Table 5.4. Body condition indices of adult reindeer collected in 1992 and 1993 from Hagemeister Island. Data are expressed as mean (+/-SD). If not otherwise indicated year of collection was 1993.

Index	Adults		
	Level of Significance[1,2]	Males	Females
Total body weight (kg)			
1992 November	*	68.8 (10.1) (n=4)	81.2 (8.5) (n=33)
1993 September	*	105.6 (18.19) (n=5)	90.8 (12.1) (n=103)
Field-dressed weight (kg) August	n.s	83.7 (22.14) (n=2)	59 (0.7) (n=2)
M.gastrochnemius (g)	*	573.4 (4.7) (n=7)	397.3 (7.0) (n=4)
Carcass weight (kg)	*	49.6 (4.1) (n=7)	34.4 (6.1) (n=4)

Table 5.4, page 2.

Index	Level of Significance[1,2]	Adults: Males	Adults: Females
Depth of rump fat (cm)			
August	*	5.3 (0.4) (n=2)	1.0 (1.4) (n=2)
September	*	2.5 (1.3) (n=34)	1.3 (1.0) (n=21)
Liver weight (kg)	*	2.6 (0.6) (n=27)	1.8 (0.4) (n=20)
Heart weight (g)	*	960 (213) (n=25)	773 (98) (n=20)
Kidney fat weight (g)	*	168 (6.5) (n=26)	80 (2.8) (n=19)
Total body length (cm)	*	173.6 (9.9) (n=26)	164.4 (5.1) (n=18)
Total femur length (cm)	*	27 (0.4) (n=11)	25.5 (0.8) (n=6)

[1]n.s. = values in the same row are not significantly different at the 5% significance level.

[2]* = values in the same row are significantly different ($P < 0.05$).

Table 5.5 Seasonal change in body condition indices for adult male reindeer collected during autumn 1993 from Hagemeister Island. Data are expressed as mean (+/-SD).

Index	Level of Significance[1,2]	Value May (n=4)	August (n=2)	September (n=1)
Field-dressed weight (kg)	n.s.	79.9 (6.3)	83.7 (22.1)	119.2
M.gastroch-nemius (g)	n.s.	588.3 (4.5)	581.5 (1.9)	498
Carcass weight (kg)	n.s.	50.9 (3.9)	50.3 (1.7)	43.1
Depth of rump fat (cm)	*	3.2 (0.8)	5.25 (0.35)	4.0
Liver weight (kg)	n.s.	2.6 (0.6)	2.5 (0.3)	3.7
Heart weight (kg)	n.s.	1.1 (0.2)	1.0 (0.2)	1.0
Kidney fat weight (g)	n.s.	195.1 (6.3)	172.5 (1.1)	150
Total body length (cm)	n.s.	170.8 (5.2)	162.6	180

[1]n.s = values in the same row are not significantly different at the 5% significance level.

[2]* = values in the same row are significantly different ($P < 0.05$).

Table 5.6. Seasonal change of body condition indices for adult female reindeer collected during autumn 1993 from Hagemeister Island. Data are expressed as mean (+/-SD).

Index	Value		
	Level of Significance[1,2]	August (n=2)	September (n=2)
Field-dressed weight (kg)	*	59 (0.7)	55.1 (0.3)
M.gastroch-nemius (g)	n.s.	347.8 (6.0)	446.8 (3.5)
Carcass weight (kg)	n.s.	30.07 (5.2)	38.64 (3.0)
Depth of rump fat (cm)	n.s.	1.0 (1.4)	0.5
Liver weight (kg)	n.s.	2.6 (0.5)	1.8 (0.02)
Heart weight (kg)	n.s.	0.793 (0.01)	0.775 (0.04)
Kidney fat weight (g)	n.s.	87.5 (1.6)	100 (3.5)
Total body length (cm)	n.s.	166.4 (5.4)	161.5 (12.0)

[1]n.s = values in the same row are not significantly different at the 5% significance level.

[2]* = values in the same row are significantly different ($P < 0.05$).

Table 5.7 Total body length (cm) and femur length (cm) of adult male and female reindeer on Hagemeister Island in comparison to data from: Nunivak[1] and St.Matthew[2] Islands. Data are expressed as mean (+/-SD).

Herd	Body Length (cm)		Femur Length (cm)	
	Males	Females	Males	Females
Hagemeister	173.6(9.9) (n=26)	164.4(5.1) (n=18)	27.0(0.4) (n=11)	25.5(0.8) (n=6)
Nunivak	175.4(6.4) (n=8)	163.4(5.1) (n=39)	27.8(0.5) (n=8)	26.1(0.78) (n=39)
St. Matthew	192.0 (n=1)	164.4(4.7) (n=9)	------	25.9(0.55) (n=9)

[1]Klein 1981

[2]Klein 1959 and 1968

Table. 5.8. Average total liveweight (kg) and weight range of male (M) and female (F) reindeer on Hagemeister Island. Comparative data is from: St. Matthew[1] and Nunivak[2] Islands; Mackenzie Delta[3], NWT, Canada, and Seward Peninsula[4]. Data for these studies were collected between July, August, September, and November.

	Body weight (kg)						
Herd	Calves		Yearlings		Adults		Period
	Males	Females	Males	Females	Males	Females	
Hagemeister	52 (32-72)	48 (26-79)	72 (56-97)	75 (53-98)	105 (86-125)	90 (52-129)	Sept.'93
	49 (37-55)	47 (36-70)	77 (61-92)	72 (65-84)	68 (54-76)	81 (70-97)	Nov.'92
St. Matthew Island					129 (86-100)	94	July'66
Nunivak Island					113	89	Aug.'65

Table 5.8, page 2.

Herd	Body weight (kg)						
	Calves		Yearlings		Adults		Period
	Males	Females	Males	Females	Males	Females	
Mackenzie Delta	40 (25-52)	35 (15-47)	74 (64-81)	69 (59-73)	129 (114-141)	86 (68-95)	July'62
Seward Peninsula	26	25	67 (60-93)	62	121	83	June'92

[1]Klein 1959 and 1968

[2]Klein 1981

[3]Krebs and Cowan 1962

[4]Blodgett et al. 1994

Chapter 6
Population Dynamics of Reindeer on Hagemeister Island

Reindeer have been introduced to eight Alaskan islands since 1911 (Table 6.1). The main objective of these introductions was to provide Alaskan Natives with the opportunity to establish a Natively-owned reindeer industry and provide them with an alternative source of meat (Stern et al. 1980; Palmer 1934). These islands differ in size, latitude, and ecological complexity. However, the absence of natural large predators is common for all. Food resources, in particular lichens during winter, climate, diseases, and level of management are thought to be the main limiting factors for these reindeer populations (Scheffer 1951; Klein 1968). The typical response by a population liberated or introduced into previously unoccupied areas is an eruption, followed by a decline and finally relative stability in which the population density remains below the peak density (Riney 1964; Caughley 1970). The reindeer populations on Nunivak, Umnak, and St. Lawrence Islands appear to have followed Riney's (1964) model. The reindeer populations on the Pribilof and St. Matthew Islands, however, showed different responses. For unknown reasons, the St. George reindeer population showed a dampened eruption. On St. Paul and St. Matthew Islands, reindeer populations erupted and subsequently crashed to very low numbers (Scheffer 1951; Klein 1968). A combination of depleted lichen winter range, adverse weather, and in the case of St. Paul Island, poaching were implicated as causes of the population crashes.

Reindeer were introduced to Hagemeister Island in 1965 and 1967[1]. A summary of the historical background of this

[1]Grazing permit by BLM (in BLM and US-F&WS files).

reindeer herd is given in Table 6.2. Since introduction in 1965, reindeer numbers grew from 144 to 1,011 head in 6 years. The censuses (post calving from 1972 until 1989) showed that animal numbers declined then and appeared to remain steady at about 724 +/- 127 (mean +/- SD)) head. By 1990, the herd had reached an all time high of 1,530 animals (Table 6.3). To help understand the population dynamics of Hagemeister Island reindeer it was decided to built a reindeer population simulation model. The aims of this study were to: (1) build a simulation model of the Hagemeister Island reindeer herd; (2) document mortality and pathological conditions; and (3) describe the seasonal range use pattern, and social organization of the Hagemeister Island reindeer herd.

Methods

See Chapter 3 for a description of the aerial census methods.

Statistical Analysis

Least squares regression analysis was used to compute fitted linear models for data on population growth (Zar 1984). The level of significance was $P < 0.05$.

Simulation Model

A single species model using a Quattro® spreadsheet was developed. The main objective of the model was to simulate the Hagemeister Island reindeer population. Because little is known about the ecology of this herd it was decided to build a simple single-species model. Detailed information on the Hagemeister Island reindeer population (i.e. age-specific mortality and pregnancy rate, and age and sex

composition of the herd in different years) is lacking. Thus my model only differentiated between 3 age classes: calves, yearlings, and adults, for the two sexes. In the model, surviving calves are recruited in the yearling age class and yearlings into the adult age class after one year. Adults stay in the adult age class until they are harvested or die. However, the model is limited in that it does not specify or account for the age when animals enter into an old age category and are then eliminated from the herd. To create population fluctuations, natality and mortality were built into the model. The time step to calculate change in the reindeer population is one year. The model is initialized with an estimate of population size, sex, and age structure.

Population Size

The model used the known number of individuals of both sexes introduced in 1965 and 1967 (Table 6.1). The actual population estimates for Hagemeister Island reindeer were used as checks for the population size generated by the simulation model (Table 6.3).

Sex Ratio and Fecundity

In reindeer, the sex ratio of calves at birth is 1:1 (Leader-Williams 1988; Roine 1974). Thus, a sex ratio of 1:1 for calves at birth was assumed for the model. There is evidence that male calves may have a higher postnatal mortality than female calves (Chetkiewicz 1993). This shifts the sex ratio towards males in yearling age class (calves that survived from the previous year). However, since no information was available on differential mortality for the Hagemeister Island herd and for the sake of simplicity a sex ratio of 1:1 was assumed for yearlings. Female reindeer

attain physiological puberty usually as yearlings (Leader-Williams 1988; Roine 1974). However, they can conceive as calves (Roine 1974; Ropstad et al. 1991). Early sexual maturity and high pregnancy rates are thought to reflect good nutritional food and/or body condition (see Chapter 4). It is quite likely that breeding of calves had contributed to the high rate of increase during the early years after their introduction to Hagemeister Island. However, it was difficult to determine when range conditions would have deteriorated enough to make conceptions in calves unlikely. For the modeling I decided to exclude calves from breeding and only include yearling and adult breeding. There is no evidence that fecundity in reindeer declines with progressive age at least up to 9 year old females (Chetkiewicz 1993) and in caribou up to 15 years old (Dauphine 1976; Quellet 1992), however, fecundity of yearlings is thought to be slightly lower than in females > 2 years old (Leader-Williams 1988; Dauphine 1978). Although there is no evidence that fecundity declines with progressive age it is likely that it will vary. Several studies with caribou have shown that females who had reared a calf were in poorer condition at the beginning of the breeding season and were less likely to conceive than females who had not reared a calf in the same year (Adamczewski et al. 1987b; Allay-Chan 1991; Cameron et al. 1993). Breeding between alternate years for highly reproductive females has been linked to poor condition prior to the breeding season (Thomas 1982). Furthermore, a decline in fecundity has been demonstrated in Norwegian reindeer under poor grazing conditions (Skogland 1985b, 1990). This decline in fecundity was associated with loss of body condition caused by increased tooth wear at an earlier age,

due to low quality forage (Skogland 1985b, 1990). Under this circumstance, mortality possibly increases in older females (Skogland 1985b). However, no information about the productivity of female reindeer on Hagemeister Island was available. For the model, I decided to assume that subadult fecundity was lower than adult fecundity and that adult and subadult fecundity was constant. The initial estimates were obtained from Leader-Williams 1980 and 1988) and were 0.90 and 0.85 for adult and yearling females, respectively.

Mortality

Following birth, both calf and adult mortality estimates were subtracted from the population to obtain survivorship. Disease and predation, together with limited food resources are recognized as important density-dependent factors that limit *Rangifer* populations (Klein 1968; Leader-Williams 1988; Bergerud 1974). Density-independent factors such as weather can be an important limiting factor depending on the circumstances (see Chapters 1 and 3). The importance of each of these factors in contributing towards mortality varies between different reindeer populations. In this study, carcasses (natural death or sacrificed) on Hagemeister Island were examined. Age, sex, pathological conditions (i.e. broken bones and dental anomalies), and location of skeletal remains (topographical map 1: 63,000) were recorded for each carcass found during field surveys in 1992-1993. For fresh carcasses, routine post mortem examinations were performed and pathological conditions were noted (Jones and Hunt 1972). Location of casted antlers were also recorded (topographical map 1:63,000). Animals $\leq$ 5 years old were aged on the basis of incisor tooth eruption and tooth wear (Palmer 1934; Skjenneberg and Slagsvold

1968). Animals > 5 years old were not aged further and classified as 5^{+}. Sex determination on skeletal remains was based on disparity in antler size and morphology, pelvic bones, and genitals, if present. Sex determination was deferred for questionable cases. Several factors may affect the patterns and causes of mortality on Hagemeister Island. First, there was a native population of red fox and brown bears which apparently swim from the mainland to Hagemeister Island. On the Seward Peninsula, Alaska, predation by foxes and brown bears was identified as an important cause of reindeer calf mortality (Chetkiewicz 1993). Secondly, the Hagemeister Island herd was harvested by Native Herders from the village of Togiak. Thirdly, the reindeer population on Hagemeister Island was established on a small original population. Inbreeding can have deleterious effects upon reindeer and may influence patterns of mortality. Renecker and Blake (1992) reported several cases of albinism in conjunction with other congenital defects in reindeer calves on the Seward Peninsula, Alaska.

Calves

There is no information that foxes and brown bears on Hagemeister Island influence reindeer calf survival. Thus it was decided to use an initial estimate for mortality rate for calves from reindeer herds that lack predators. An initial estimate (0.2) was obtained from Leader-Williams's study of reindeer on South Georgia Island (1980, 1988). In his study, accidents (i.e. drowning, cliff falls, and avalanches), hypothermia, calf abandonment, and starvation during winter were assumed to be the main causes of mortality.

Adults and Yearlings

Mortality of reindeer increases progressively with age, and differs between the sexes (Leader-Williams 1980; Reimers 1977, 1982). Main causes of death of predator-free reindeer populations have been attributed to diseases, starvation during winter due to limited food resources, accidents, and old age (Gates et al. 1986; Klein 1968; Leader-Williams 1980, 1988; Reimers 1977, 1982). For Hagemeister Island reindeer, no information was available about differences in life expectancy of males and females of different ages. However, to account for the known differential mortality between the sexes in adults (Klein 1968; Gates et al. 1986; Leader-Williams 1980) a higher mortality on a yearly basis was assumed for adult male than adult female reindeer on Hagemeister Island. For yearlings there was no conclusive evidence that there is a differential mortality between the sexes and was not differentiated in this model, but was assumed to be lower than adults (Leader-Williams 1988). Mortality rates were obtained from Leader-Williams's study of reindeer on South Georgia Island (1988) and were 0.35 and 0.33 for adult male and females, respectively, and 0.1 for all yearlings. Mortality in wild reindeer and caribou populations is thought to fluctuate from year to year (Bergerud 1971; Gates et al. 1986; Leader-Williams 1980; Reimers 1977, 1982). However, because of lack of data on the magnitude of mortality between-year fluctuations it was decided to assume that mortality remained constant on Hagemeister Island.

Annual Harvest

Since the introduction of the herd in 1965, Native herders from the village of Togiak managed the

Hagemeister Island reindeer herd. Travel to the island was by boat or fixed-wing aircraft. There was no information available on time of the year reindeer were harvested from Hagemeister Island. However, logistics and seasonal biology of reindeer on Hagemeister Island restrict harvest presumably to the summer and winter. During spring and autumn, gale force winds occur frequently and make travel by boat hazardous. Thus travel to the island by boat is limited to the summer. However, number of reindeer harvested during that period is restricted, because the village infrastructure lacks adequate storage and cooling facilities for large numbers of carcasses[1]. During the winter, travel to the island is by airplane. However, travel is expensive, restricted to light aircraft, and only a few landing sites are available on the island. It is assumed that females were only harvested during the summer, presumably starting about 6 weeks after peak calving until late August, just prior to the beginning of the breeding season. The benefits of this harvest strategy were: (1) females were not harassed prior to calving which could result in late-term abortions (Skjenneberg and Slagsvold 1968); (2) it reduced the risk for calf abandonment; and (3) calves were at least 6 weeks old and would have started to graze. This increases calf survivorship in case their mothers are harvested. For males, harvest could have taken place either in summer or winter. However, bulls are in prime body condition prior to the rut (Leader-Williams 1988). Thus harvesting bulls during this time would result in greater carcass yields, however, it is unlikely that bulls were harvested during the rut since it would disrupt breeding and meat quality would be low (Curnew

[1]1987 letter by D. LaPlant to J. Martin (in BLM and US-F&WS files).

and Lear 1980). Liveweights in reindeer on the Seward Peninsula, peak in bulls 4-5 years of age and in females 8 years of age (Blodgett et al. 1994). For the model, it was assumed that yearlings were not harvested, but only male and female adults (> 2 years old). Furthermore, it was assumed that more males than females were harvested (ratio 3:2). The benefits of this harvest strategy would be: (1) continued rapid growth rate of the herd; (2) a favorable bull : cow ratio; for example a surplus in breeding males can interfere with breeding dates (L. Adams pers. commun. 1992); and (3) greater average carcass yields.

The following historical events were incorporated into the simulation model. In 1987, no animals were harvested. In 1988, the reindeer herd was reduced by 400 animals (composition unknown). Three hundred of the 400 reindeer were harvested and about 100 were airlifted to a deer farm in Palmer (D. Tomlin pers. commun. 1993). For the model I assumed that: predominantly females (breeding stock) were airlifted (n=100); and for the harvest of 300 animals that more males were harvested (3:2). During the winter of 1991-1992, approximately 300 reindeer died, primarily adult males.

Equations

For the simulation model the following formulas were used:

(1) Number of spring calves:

Number of females (c) * fecundity rate + Number of yearlings/2 (c) * fecundity rate

(2) Number of summer calves:
Number of spring calves (c) * mortality rate

(3) Number of yearlings:
Number of summer calves (**p**) * yearling mortality

(4) Number of male adults:
Number of yearling (**p**)/2 + Number of adult males (**p**) * mortality - annual harvest (**c**)

(5) Number of female adults:
Number of yearling (**p**)/2 + Number of adult females (**p**) * mortality - annual harvest (**c**)

(6) Summer population size:
Number of summer calves (**c**) + Number of yearlings (**c**) + Number of male adults (**c**) + Number of female adults (**c**), where **c** stands for current year and **p** for previous.

Sensitivity Analysis

Preliminary runs of the model indicated that in order: to reach a population size of 1,011 head by 1971 the initial estimates for mortality rates of adults and calves were too high. Therefore, I modified the mortality estimates to 0.1 and 0.07 for males and females, respectively, and 0.1 for calves for the period 1965-1971. These values are comparable to values reported by Bergerud (1971) for Newfoundland caribou. The initial fecundity rate for adult females (0.9) and yearlings (0.85) remained unchanged.

Only a very limited annual harvest (< 20 animals) could have taken place before the year 1972. With a harvest rate > 20 animals, adult fecundity had to be increased to 0.96

and/or adult mortality lowered to 0.04 and 0.02 for males and females, respectively. Therefore, no harvest was built into the model during 1965 - 1971. Annual harvest was initialized in the model in the year 1972.

In order to reproduce the 1988 harvest and the 1991-1992 winter die-off of approximately 300 predominantly adult males, annual harvest rates in previous years could not be biased towards males. Therefore, I modified the sex ratio of the annual harvest to 1:1.

To reproduce the 1990 population size of 1,530 head, biological parameters in the simulation model declined beginning in the year 1972. The magnitude of the decrease was dependent on annual harvest rate (Table 6.4). These new values are comparable to values reported by Bergerud (1971) for Newfoundland caribou, for reindeer on South Georgia Island (Leader-Williams 1988), and for reindeer on Svalbard Island (Reimers 1982, 1983).

Results

Population Estimates

Censuses

The population growth rate of reindeer since introduction in 1965 until 1971 averaged 46% (r^2 = 0.98; SE_b = 0.18 ; $P < 0.001$). In this regression analysis, the curve was constrained to pass through the known number of reindeer > 1 year old (post calving census). The regression equation was $\mathbf{y = 4.26 + 0.412x}$, where, x is the years since introduction. Regression of number of reindeer on years for the period 1972 until 1984 was not significant. This indicated that the herd did not grow and herd size remained steady. No post calving censuses for the period from 1985 until 1988 were available. For a matter of consistency, it

was decided not to use the precalving censuses for a regression analysis for this period. However, the precalving census suggested that the herd size increased during this period. By 1990, the herd reached 1,530 head. In both 1991 and 1992, herd size declined. The decline in numbers can be attributed to the 1991-1992 winter die-off and culling during November 1992.

Simulation Model

The population estimates generated by the model for the Hagemeister Island reindeer suggest a growing herd (Table 6.4). The population growth rate (for the model with an annual harvest rate of 50 animals) since introduction in 1965 until 1971 averaged 46% (r^2 = 0.96 ; SE_b = 0.28 ; $P < 0.03$). In this regression analysis, the curve was constrained to pass through the known number of reindeer > 1 year old generated by the simulation model. The regression equation was **y = 4.48 + 0.443x**, where x is the years since introduction. Regression of numbers of reindeer on years for the period 1972 until 1984 was significant (r^2= 0.99; SE_b = 0.011; $P < 0.003$; **y = 6.94 + 0.0275x**). This indicated that the herd was growing. The predicted annual population estimates are higher than actual census data. This suggests that annual aerial censuses may have been inaccurate.

Mortality

Causes of mortality

In late winter 1991-1992, a die-off of approximately 300 animals occurred. The cause of death appeared to be starvation. Mature males constituted the majority of carcasses (see Chapter 3). In late winter 1992, an estimated 842 animals were cropped (742 shot by the US-F&WS and 100 by

a private individual) and 122 animals were airshipped to Goosebay, Alaska (70% calves, 25% cows, and 5% bulls) (R. Stimmelmayr pers. commun. 1992). In fall 1993, 289 reindeer were shipped from Hagemeister Island to Project Hope and 135 cropped (R. Stimmelmayr pers. commun. 1993). In addition, 16 animals (1 calf, 4 adult females, and 11 bulls) were collected for research purposes during 1992 and 1993. The population composition in 1992 was 31% calves, 38.3% females (yearlings and adults), and 29.8% males (yearlings and adults). The total herd size was approximately 1,200 animals (850 cropped, 122 shipped to Goosebay, and 203 remained alive on the island). The population estimate was based on age and sex distribution of examined carcasses (n_1=284) and shipped (n_2=122) animals. Total sample size was 406 animals. The age structure of the 184 carcasses that were examined was : 19% calves, 30% yearlings, 18% 2.5 year olds, 13% 3.5 year olds, 17% 4.5 year olds, and 2% ≥ 5.5 year olds. The sex ratio of calves was: 1:1; of yearlings: 59% males to 41% females; and 39% males to 61% females in > 2 year olds. Following the 1992 airlift of animals to Goose Bay and culling of a large proportion of the herd, the 1993 population composition changed. Total herd size was approximately 325 animals, with 37.5% calves, 51.4% females, 9.2% males, and 1.9% of undetermined gender.

Pathological Conditions

Skin warbles flies and nasal bot flies were present on Hagemeister Island. Infestation levels are much lower than observed in reindeer on the Seward Peninsula (Dieterich 1981). Number of skin warble flies ranged between 50 and 150 larvae per animal. The number of nasal bot flies per animal ranged between 10-35. No cases of lungworms (*Dictyocaulus*

spp.) were observed in animals from Hagemeister island. Gastrointestinal parasites found in reindeer (n=15) included *Ostertagia* spp., *Nematodirella* spp., and *Eimeria* spp. There were between 50 and 100 eggs of nematodes per gram feces. For coccidia, eggs per gram feces ranged between 50-750 cysts. One case of cystic hydatid disease (*Echinococcus granulosus*) was observed. The cyst was located in the liver. *Sarcocystis* spp. cysts were found in the myocardium of several animals. Contrary to most mainland populations no cases of brucellosis (*Brucella suis biovar IV*), external or systemic necrobacillosis (*Fusobacterium necrophorum*), or skin warts (*Papillomatosis*) were observed. One animal had a small mandibular lesion associated with the second premolar. One female had a 20 x 20 cm large external ventro-abdominal tumor. The mass consisted of densely organized fibrotic tissue. It is thought that the mass could be a sequel of a previous goring injury. Another more recent inguinal goring injury was observed in a mature bull. Several cases of keratitis (white eye disease) were observed. The majority of cases occurred in calves.

Social Organization, Distribution, and Group Size

Reindeer were sexually segregated by November (1992) and moved into large cow/calf and yearling aggregations or smaller groups of young and adult bulls. Approximately 10-12 individual herds, ranging in size from 30-400 animals were located in the south central portion of the island. Mixed groups of cows and bulls were observed by late August (1993). Mature reindeer bulls on Hagemeister Island entered rut about the first week of August. Approximately 25-30 individual herds, ranging in size from 10-70 animals were widely dispersed across the southern portion of the island.

The group size and distribution of the herd differed between the different seasons on the island (Table 6.6; Figs.6.1-6.3). Group size tended to be greatest during late winter (January-February) and summer (June-August). A decline in average group size and increased dispersal was noted by late February. The distribution of carcasses and antlers found during 1992-1993 is shown in Fig.6.4.

Discussion

Social Organization, Distribution, and Group Size

There seems to be a difference in winter and summer distribution of animals. On the basis of surveys, animals used four areas of which two overlap during both seasons. The location of the winter range is similar to the area identified as winter range of bulls on the basis of accumulation of casted antlers. In April and May, the herd appeared to use the entire island. There is no conclusive evidence that cows concentrate in a particular calving area. In this study, males and females, excluding the rutting season, were segregated. Predation has been mainly used to explain sexual segregation in *Rangifer* (Jakimchuk et al. 1987). For the Hagemeister Island population, predation appears to be an unlikely cause. However, it cannot be completely excluded. There is a red fox population and brown bears apparently swim from the mainland to Hagemeister Island. In contrast to caribou on Coats Island, Canada (Gates et al. 1986), reindeer on Hagemeister Island tended to move in large aggregations during mid winter similar to continental caribou populations (Table 6.6). In winter, food distribution due to snow, is usually limited to xeric ridge tops (Klein 1959) and aggregation of reindeer is the usual tactic. By the end of February, group size decreased and

dispersal increased (Fig 6.1-6.3). Skogland (1989) suggested group size is reduced during winter when food abundance on ridges declines. Group size on Hagemeister Island remained small until the end of May. Differential phenological progression of plant growth within the habitat is thought to be the underlying cause (Skogland 1989). Wild reindeer follow this phenological progression by selective foraging. By June, reindeer on Hagemeister Island coalesced into large post-calving aggregations. This behavior continued until late summer (July) when group size again started to decrease. This suggests that plant growth had ceased on Hagemeister Island and senescens had begun to occur in all food patches such that differences in quality between habitats was reduced (Skogland 1989).

Population Dynamics of Reindeer on Hagemeister Island

Censuses

From the time of introduction in 1965 to 1971, the reindeer herd on Hagemeister Island was in the initial phase of eruption (Riney 1964). The population growth rate averages 46% per year over this period and exceeds reported estimates of population growth for other artic insular *Rangifer* populations: for example Southampton Island, 27.9% (Quellet 1992), St. Matthew Island, 34% (Klein 1968), and the Pribilof Islands, 33-36% (Scheffer 1951). This suggests possible ecological or genetic differences between the different herds. The 1972 and subsequent censuses indicated that the herd was declining, and suggested a dampened oscillation. In 1990, the herd size was estimated to be 1,530 animals and suggested a second eruption.

Simulation Model

Reindeer population estimates based upon censuses were comparable to those generated by the model (Table 6.4). However, the model estimated a population size during the period of 1972-1989 that was higher than actual census data. Thus, the model indicated that annual aerial censuses may have been inaccurate. It is most likely that herd size was repeatedly underestimated. Biases in aerial transect surveys conducted on moose during May and June have been reported (Gasaway et al. 1985). The extreme fluctuations of the annual growth rates from 1972-1992 also support this conclusion (Table 6.3). Based on the known logistic difficulties that are involved in the harvest of reindeer from this remote island it is assumed that an annual harvest rate > 150 animals is unrealistic. An annual harvest rate ranging ≥ 50 and < 150 is more likely. The model indicated that by 1972 demographic rates such as survival rates and fecundity rates were decreasing (Table 6.4). The magnitude of the decrease would be dependent on annual harvest rate. Skogland (1985b, 1990) suggested that numbers of wild reindeer living in predator-free habitats are regulated by food levels in a density-dependent manner and that these changes occur mainly at high population levels or close to ecological carrying capacity. The effects of density-dependent resource limitations are decreased juvenile survival, lowered subadult fecundity, body size decrements, increased male mortality, and later calving times (Skogland 1983, 1985b, 1986, and 1990). The model suggests that the Hagemeister Island reindeer herd experienced density-dependent effects. If I assume the decline in the carrying capacity of winter lichen range was the most important regulator of reindeer on Hagemeister Island, then, were any

of the above density-dependent effects present?

The age structure of Hagemeister Island population suggests that the herd was slowly increasing. The proportion of calves in this sample is presumably under estimated. First, at least 80 calves were shipped during November, 1992 prior to cropping and carcasses of shot young winter calves were small and more likely to be overlooked (Leader-Williams 1980). The biased sex ratio of shot carcasses (n=184) and the winter die-off 1991-1992 (see Chapter 3) towards a predominance of females over males in > 2 year old age class suggests that males on Hagemeister Island had a higher mortality rate than females.

The females on Hagemeister Island, first bred at the normal age for the species (1.5 years old). Interestingly, > 50% and about 25% of the 1992 and 1993 yearlings, respectively, apparently attained puberty as calves. This was surprising as high density levels were present during both years. Possible explanations for this phenomena have been presented in Chapter 4. Herd productivity was > 70%, based on the herd composition counts in 1992 with an estimated calf count of 127 calves to an estimated 160 females. This rate was similar to calving success of reindeer herds on the Seward Peninsula (McIntyre et al. 1994; Renecker and Chetkiewicz 1993). It was also comparable to the range reported for Alaskan reindeer (70% - 90%) by Hadwen and Palmer (1922). Peak calving time on Hagemeister Island is approximately 1 month later than for reindeer on the Seward Peninsula (Chapter 4). However, Hagemeister Island reindeer are caribou x reindeer hybrids, and the apparent delay maybe linked to genetics.

Although Hagemeister Island reindeer differ in body size and condition from Nunivak Island animals, the differences are small (Chapter 5). These results suggest that the Hagemeister Island reindeer experienced some food limitation effects after over-grazing lichen on the winter range. However, the effects appear to be less pronounced than expected in view of the overall poor lichen range present on Hagemeister Island. This suggests that either range quality on Hagemeister Island has not been reduced sufficiently or that Hagemeister Island reindeer do not solely depend on lichen and utilize other forage plants throughout the year. The latter would indicate that ecological carrying capacity estimates for Hagemeister Island have been previously underestimated. Several studies have shown that continental and insular reindeer populations living in lichen depleted habitats show an increase in habitat niche breadth and utilize other forage during the winter, if available (Leader-Williams et al.1981; Reimers 1977; Staaland et al. 1991; Skogland 1984). In lichen-free habitats, graminoids or moss constitute the main food item in the winter diet of *Rangifer* (Leader-Williams 1988).

A possible answer for the question whether winter lichen resources limit high-arctic *Rangifer* population may be found in the co-evolutionary relationship of *Rangifer* and lichens (Andreev 1984; Klein 1982). *Rangifer* probably originated in Beringia and the Mountains of northeastern Asia (Altai) (Guthrie 1968; Kurten and Anderson 1988). Conditions of the Pleistocene stepe were probably more moderate and vegetation in the region consisted of a supalpine flora of grasses and forbs (Kyle 1987; Sturdy 1972). *Rangifer* presumably evolved to fill a lichen-based northern food niche essentially unoccupied by other herbivores. The high digestibility of

lichens and ability of Rangifer to locate lichen beneath the snow cover is thought to reflect this relationship (Luick 1977). However, in comparison to other foraging plants lichens have extremely slow growth rates (Palmer and Rouse 1945; Andreev 1984). Therefore, lichen recovery after over-grazing, trampling or fire is considerable and may extend over decades (Swanson and LaPlant 1987; Klein and Vlasova 1991). *Rangifer* occur in habitats ranging from taiga woodlands to high-arctic islands (Bergerud 1977; Klein 1968; Leader-Williams 1988; Skoog 1968). In these alpine and arctic regions, winter range is greatly influenced by snow and ice conditions. Thus foraging by reindeer is usually restricted to areas accessible, windswept, and/or with limited snow fall (Adamzweski et al. 1988; Klein 1968; Thing 1977, 1984; Tyler 1987). By nature of their exposure, these areas are flats and ridges that support mainly xeric plant communities such as lichens and willows. This suggests that the key to species utilization by *Rangifer* lays in the relative availability of forages as proposed by Bergerud (1977) rather than dependence on a particular diet. Consequently, lichens are the primary food in most arctic and alpine habitats occupied by reindeer and caribou, because of their widespread distribution and relative abundance. *Rangifer* populations living in habitats which predominantly support lichens are limited by these lichen resources. However, mainland populations can expand their seasonal range use in response to declined food resources. Thus dampening the limiting effect of food resources (Fleischmann 1990). For *Rangifer* populations living on high-arctic islands range expansion is limited by the geography of the island. Furthermore, climatic conditions on arctic islands tend to be harsher than continental ones (i.e.

higher humidity, cooler temperatures, and more windy). *Rangifer* population living on arctic islands which predominantly support lichens, such as St. Matthew Island, and St. Lawrence Island, are more susceptible to starvation under conditions of food shortage.

I therefore conclude that area-specific climatic conditions and topography, floral diversity and productivity, possibility of range expansion and dispersal, and concrete accessibility of winter forage other than lichens are the essential modifying factors, by which *Rangifer* populations can exist in lichen-free habitats.

Table 6.1. Alaskan Islands where reindeer (RD) were introduced.

Islands	Year	Area (ha)	Number introduced
Nunivak[1]	1920	427,115	81 female RD
	1925		10 male caribou
	1928		523 female RD
St. Lawrence[2]	?	?	?
Umnak[2]	1913	100,000	86 RD
Atka	?	40,486	?
St. Paul[3]	1911	10,729	11 female RD
			5 male RD
St. George[3]	1911	9,069	12 female RD
			3 male RD
St. Matthew[4]	1944	33,166	24 female RD
			5 male RD
Hagemeister[2]	1965	27,126	51 female RD
			20 male RD
	1967		73 female RD

[1]Palmer 1934

[2]Swanson and Barker 1991

[3]Scheffer 1951

[4]Klein 1968

Table 6.2. Summary of the historical events of the Hagemeister Island reindeer herd[1,2].

Year	Event
1965	First shipment of reindeer to Hagemeister Island. Carrying capacity for Hagemeister island estimated to be 1000 animals. Land management authority is with the Bureau of Land Management (BLM).
1967	Second shipment to Hagemeister Island.
1973	First report on over-grazed lichen sites on the island. Estimate of carrying capacity for Hagemeister Island is lowered to 450 animals.
1980	Land management authority for Hagemeister Island is transferred by Congress to the US-F&WS.
1987	Range survey conducted by the USDA-Soil Conservation Service (USDA-SCS) concludes lichen ranges are severely over-grazed and reduction of herd is recommended to 200 animals (Swanson and LaPlant 1987).
1992 July	Range and Reindeer Survey in response to 1991-1992 winter die-off of approximately 300 animals (Swanson and Barker 1993; Stimmelmayr and Renecker 1992). Swanson and Barker (1993) conclude that recovery of lichen range requires approximately 150 years and recommend removal of entire herd or reduction of herd size to 50 animals. In addition, they anticipate further die-offs during the coming winter. Stimmelmayr andRenecker (1992) suggested a study of the herd based on their results, which did not clearly indicate whether the herd was *defacto* nutritionally stressed and above carrying capacity (see Chapter 3).

Table 6.2., page 2

Year	Event
1992	
November	US-F&WS harvests 750 animals. Only approximately 200 carcasses were distributed to local villages. The remainder of the carcasses are left on the island. One hundred and twenty animals were airlifted by a private individual and approximately 100 head were slaughtered by the same person. An estimated 200 reindeer remained on the island as cropping was halted due to severe winter storms.
1993	
February	Hagemeister Island Reindeer Conference, Togiak, Bristol Bay. At this meeting, the Service (US-F&WS) determined that continued grazing of reindeer on the island is incompatible with the purpose of the Alaska Maritime National Wildlife Refuge. Thus all reindeer from Hagemeister Island were to be removed. Following this meeting a cooperative agreement between US-F&WS and Reindeer and Game Farming Research Program, University of Alaska, Fairbanks is reached to conduct a study on the ecology of the Hagemeister Island reindeer herd.
August	One hundred and thirty-five reindeer were harvested by the US-F&WS. Carcasses were distributed to local villages. Two hundred and eighty-nine reindeer were airlifted to Project Hope on the mainland (R. Stimmelmayr pers. commun. 1993).
1994	A few reindeer appear to have remained on the island.

[1]Source: BLM and US-F&WS files
[2]R. Stimmelmayr pers. commun. 1994

Table 6.3. Hagemeister Island reindeer population[1].

Year	Number of Animals: Postcalving	Number of Animals: Precalving	Growth Rate (%)
1965	71		
1966	80	71	12.7
1967[3]	178		122.5
1968	234		31.5
1969	---		----
1970	443		----
1971	1,011		128.2
1972	800		-20.9
1973	455		-43.1
1974	867		90.5
1975	867		----
1976	854		1.5
1977	760		-11.00
1978	632		-16.8
1979	665		5.1
1980	650		-2.3

Table 6.3., page 2.

	Number of Animals		Growth Rate[2]
Year	Postcalving	Precalving	(%)
1981			
1982			
1983	770		
1984	590		-23.4
1985		733	
1986		650	
1987		773	
1988		1,061	
1989	784		
1990	1,530		95.2
1991	952		37.8
1992	728		-23.5

[1]Source: BLM and US-F&WS files

[2]Growth rate: number of animals minus number of animals (previous year) divided by the number of animals (previous year) times 100

[3]Second shipment 73 females

Table 6.4. Summary of biological input parameters for the Hagemeister Island reindeer population model for the period 1972-1992.

Parameter	Annual Harvest Rate (Number of Animals)			
	50	100	150	240
Fecundity Rate				
Adult	0.88	0.88	0.88	0.9
Yearling	0.86	0.86	0.86	0.86
Mortality Rate				
Calves	0.25	0.2	0.17	0.09
Yearling	0.25	0.2	0.18	0.10
Adult (male)	0.30	0.27	0.20	0.10
Adult (female)	0.22	0.20	0.15	0.08

Table 6.5. Estimates of summer reindeer population size as determined from modeling the Hagemeister Island reindeer population from 1965 to 1992.

Year	Annual Harvest Rates[1] (Number of Animals)			
	50	100	150	240
1965	71	71	71	71
1966	103	103	103	103
1967	275	275	275	275
1968	394	394	394	394
1969	551	551	551	551
1970	752	752	752	752
1971	1012	1012	1012	1012
1972	1037	1025	1014	1009
1973	1086	1047	1026	1012
1974	1090	1064	1035	1015
1975	1115	1083	1044	1018
1976	1141	1104	1055	1021
1977	1170	1128	1068	1023
1978	1201	1154	1083	1026
1979	1234	1185	1100	1029
1980	1270	1218	1121	1032

Table 6.5, page 2.

Year	Annual Harvest Rates[1] (Number of Animals)			
	50	100	150	240
1981	1309	1257	1145	1035
1982	1350	1300	1173	1038
1983	1395	1348	1206	1042
1984	1444	1403	1246	1047
1985	1496	1465	1292	1053
1986	1552	1535	1347	1061
1987	1678	1750	1618	1409
1988	1277	1441	1381	1288
1989	1353	1537	1470	1372
1990	1402	1619	1559	1475
1991	1180	1461	1440	1430
1992	1318	1632	1610	1623

[1]Annual Harvest Rate: no harvest from 1965 until 1971

Table 6.6. Group sizes of reindeer (RD) on Hagemeister Island in different seasons and years.

Date	No.of RD	No.of Groups	Mean Group Size (+/-SD)	Maximum Group Size
Dec. 92	194	9	21.6 (7.3)	49
Jan. 86	324	2	324 (111)	435
Feb. 85	733	4	183.3 (88)	410
93	72	4	18 (13.14)	33
Mar. 93	184	11	16.7 (18.4)	60
Apr. 88	1,031	52	20.2 (3.0)	100
87	748	10	75.4 (14.1)	151
May 88	826	29	28.5 (6.0)	150
93	325	14	23.2 (6.2)	70
June 93	300	1	300	300
July 91	952	5	190.4 (61.7)	372
90	1,530	10	153 (87.4)	1530
83	800	2	400	400
93	275	3	91.7 (22)	125

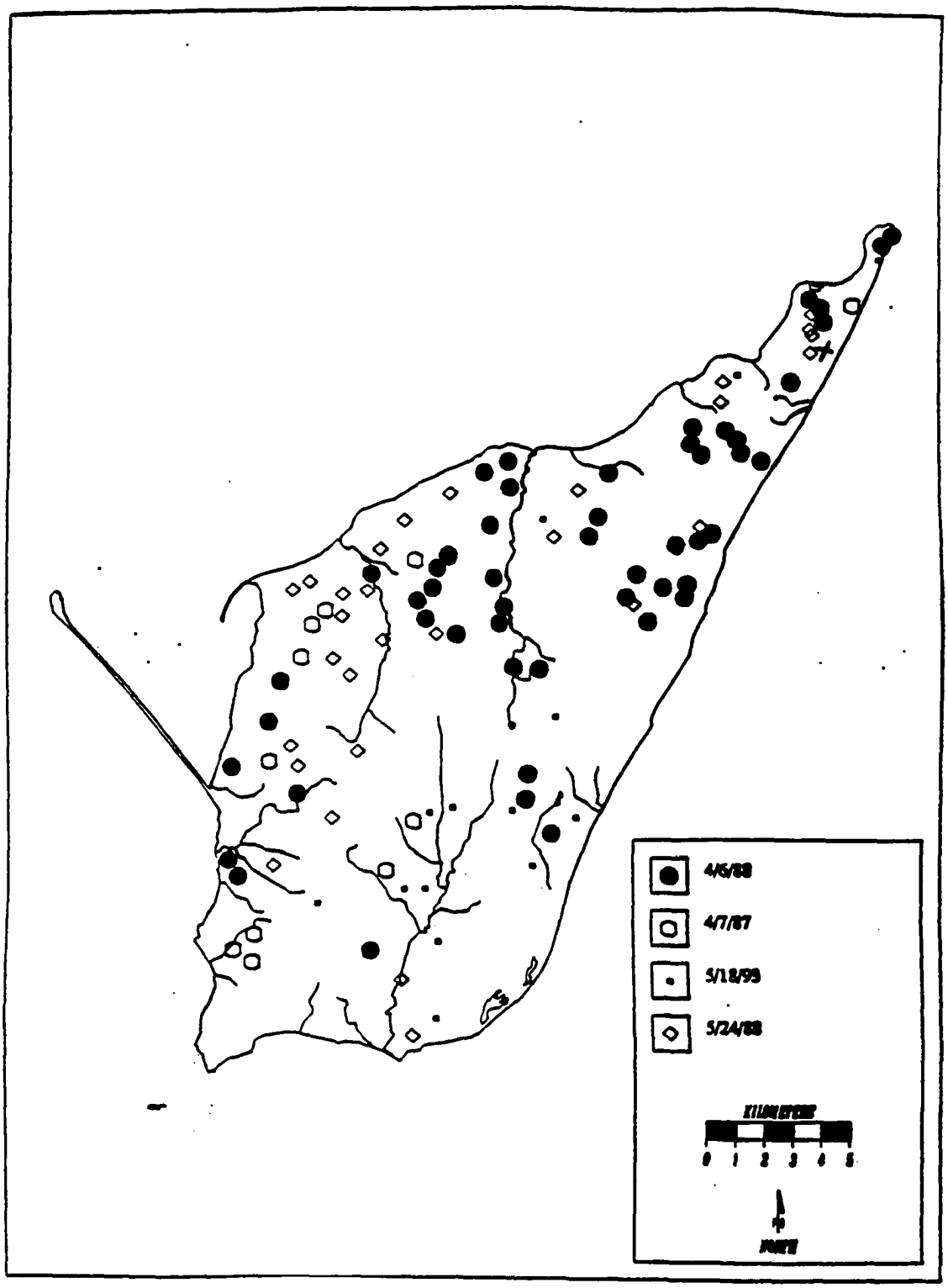

Fig.6.1. Distribution of reindeer on Hagemeister Island during spring (April-May).

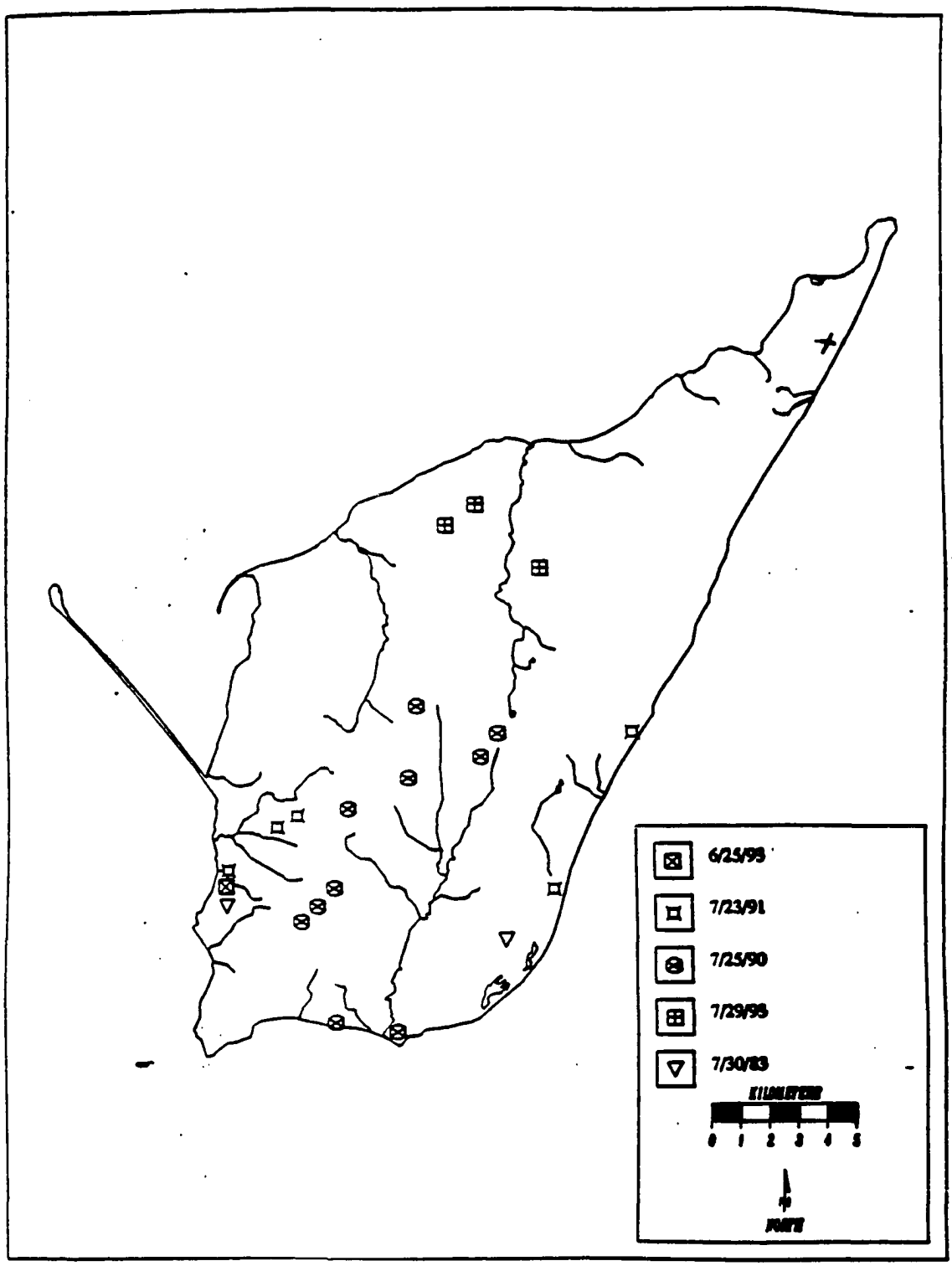

Fig.6.2. Distribution of reindeer on Hagemeister Island during summer (June-August).

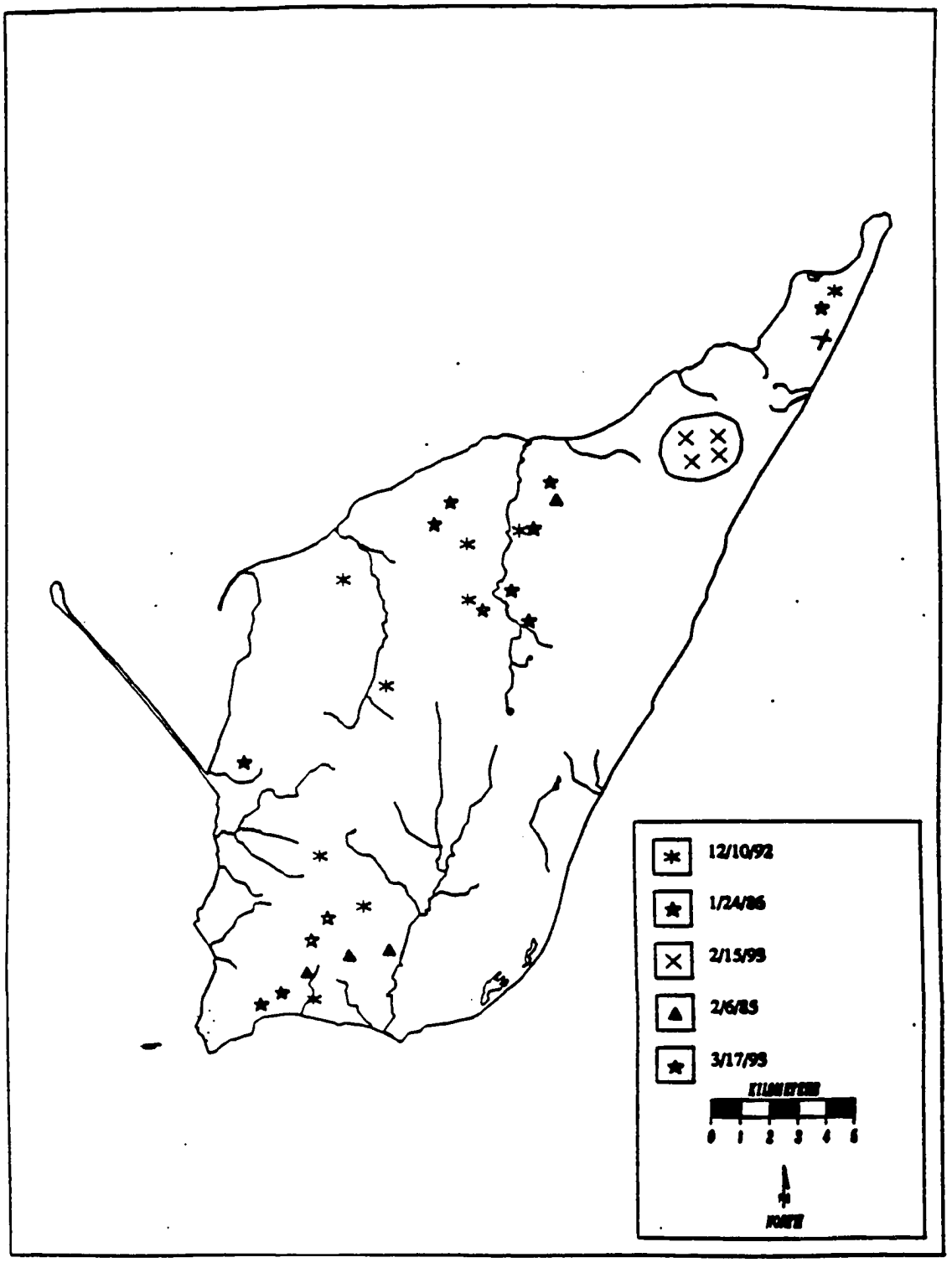

Fig.6.3. Distribution of reindeer on Hagemeister Island during winter (December-March).

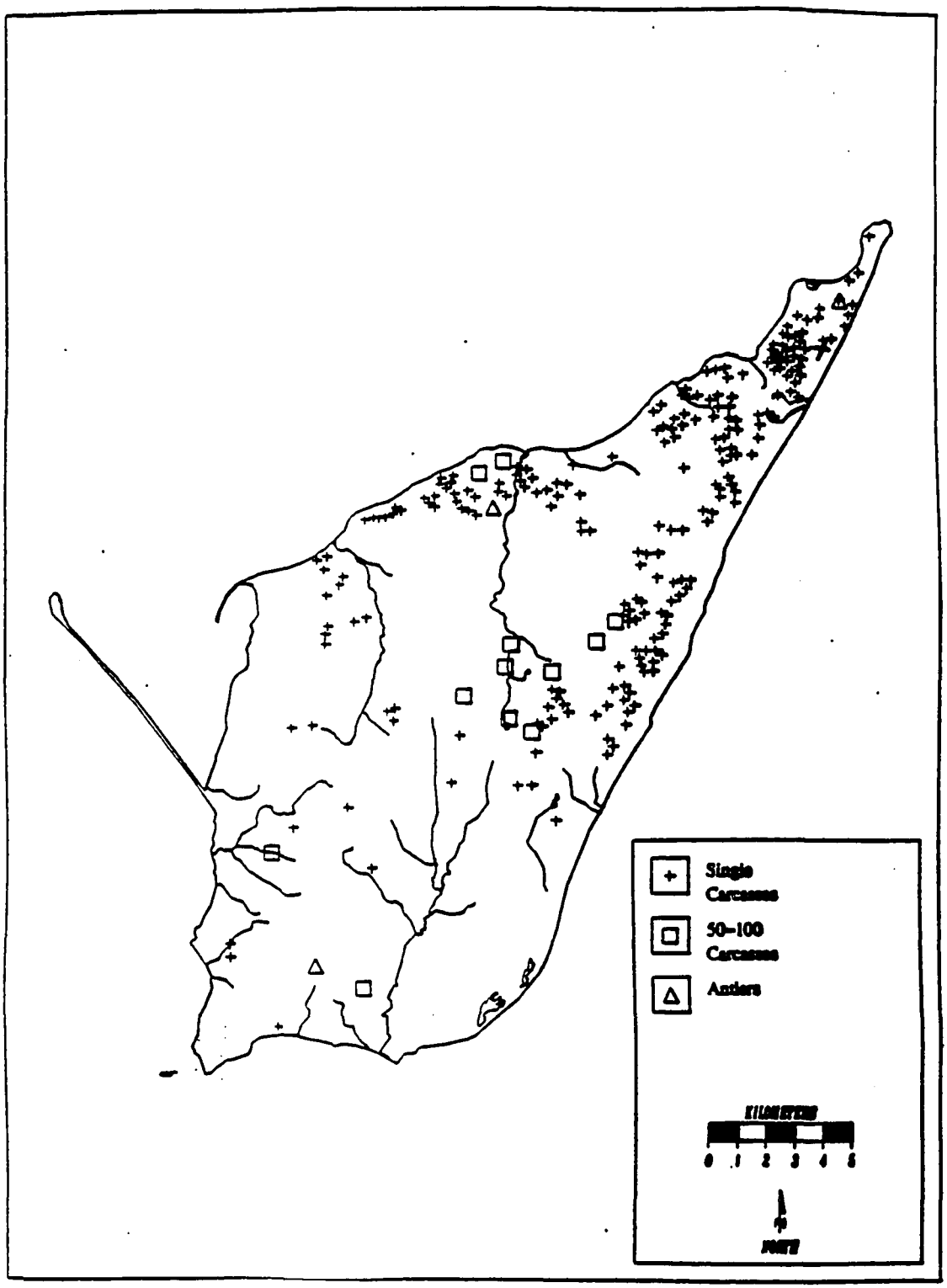

Fig 6.4. Location of reindeer carcasses from 1991-1992 winter die-off (cross) and from November, 1992 culling operation (rectangle) on Hagemeister Island.

Chapter 7
Synthesis

Introduction of herbivores, primarily reindeer and caribou have had a major impact on the biota of several arctic islands (Klein 1968; Scheffer 1951; Swanson and Barker 1991). On Hagemeister Island, grazing by reindeer has caused major changes in lichen cover (Swanson and Barker 1993). This synthesis aims to: (1) answer the main objective of this study, namely was the reindeer population on Hagemeister Island limted by winter lichen range in a density-dependent manner; (2) examine whether or not there is a biological case for active management of the Hagemeister Island herd, in the context of herd health and of conservation of the native fauna on Hagemeister Island, (3) to assess the significance of the reindeer herd for the Native community of Togiak; and (4) to assess the historical management policy of Hagemeister Island reindeer herd.

What Factors Drive *Rangifer* Populations?

Density-dependent resource limitation is thought to be the main regulating factor for *Rangifer* populations living in predator-free Arctic Islands (Gates et al. 1986; Klein 1968; Scheffer 1951). The typical reaction of a population after introduction is a rapid increase in numbers in response to the discrepancy between carrying capacity and animal numbers (Riney 1964). With increasing population density, intraspecific competition for declining food resources occurs and this regulates animal numbers (Skogland 1985b). Competition affects animal growth, fat accumulation, and ultimately, reproduction and/or animal survival. At high density, density-independent factors such as severe weather can exacerbate food limitations and/or affect animal

recruitment (Skogland 1985b). Changes in lichen availability and/or production concomitant with extreme weather conditions have been implicated as the cause of population fluctuations in several high-arctic insular *Rangifer* populations such as on St. Matthew (Klein 1968), the Pribilof Islands (Scheffer 1951), and Coats Islands (Gates et al. 1986).

Reindeer on Hagemeister Island

Reindeer were introduced to Hagemeister Island in 1965 and 1967. On the basis of aerial census data the herd erupted in 1971 and 1990 (see Chapter 6). Contrary to Riney's model (1964) the second eruption of the Hagemeister Island reindeer population exceeded the first. This suggests that range carrying capacity on Hagemeister Island had been previously underestimated and that a herd of 1,000 head did not constitute the maximum population density possible on Hagemeister Island.

The area of Hagemeister Island is comparable to St. Matthew Island and about three times larger than St.Paul Island. Although climatic conditions are more harsh on the latter islands in comparison to Hagemeister Island it is noteworthy that reindeer population densities on these islands exceeded Hagemeister Island. For example, after introduction the St. Matthew Island reindeer herd increased to 6,000 head and then crashed (Klein 1968). The St. Paul Island herd reached about 2,000 head before it started to decline (Scheffer 1951).

Results of body weight and composition suggest that the Hagemeister Island reindeer herd may have experienced some food limitation effects after overgrazing lichen on the winter range (see Chapter 5). However, the effects appear to be less pronounced than expected in view of the overall poor lichen range present on Hagemeister Island (Swanson and

Barker 1993). Overall reproductive performance of the Hagemeister Island reindeer was estimated good (see Chapter 4). It is noteworthy that a high percentage of the 1992 and 1993 yearlings had conceived. Thus there is no conclusive evidence that the herd was experiencing nutritional stress despite high population density (see Chapter 4). This suggests that either range quality on Hagemeister Island had not been reduced sufficiently to induce density-dependent effects of food limitations or that Hagemeister Island reindeer do not solely depend on lichen and utilize other forage plants throughout the year.

Extreme snowfall conditions in late winter and poor post rut condition of adult bulls appear to have precipitated the 1991-1992 winter die-off of several hundred predominantly male adult reindeer on Hagemeister Island (see Chapter 3). In reindeer/caribou, mature rutting bulls segregate from the females shortly after the peak rutting season (Skogland 1985a). The high reproductive cost during the rut leave bulls in a precarious body condition with an increased risk for mortality from malnutrition caused by severe winters (Leader-Williams 1980). Thus the circumstance of deep snow and/or icing may have hindered detection of forage, as well as access to food and resulted in starvation of bulls on Hagemeister Island.

Hagemeister Island Range

On the basis of range surveys, there is no evidence that reindeer have caused any extinction of native plant species on Hagemeister Island (Swanson and Barker 1993). Reindeer, however, have caused severe over-grazing of lichens. Erosion attributed to overgrazing amounted to < 3 ha of the Island's total 27,328 ha (Swanson and Barker 1993).

Management

Native Reindeer Herders

Since the introduction of reindeer management of the Hagemeister Island herd has been by Native herders from the village of Togiak. Management and harvest of these reindeer has been compromised by remoteness, seasonal weather conditions, and difficulty of scheduling seasonal herd management with subsistence activities. However, results of the Hagemeister Island reindeer herd simulation model suggest an annual harvest $\geq$ 50 animals $<$ 150 head (see Chapter 6). Simulation analysis of the population indicates that the herd was utilized by the local community despite logistical difficulties and suggests that reindeer herding has become integrated in the village's economic community organization.

Agencies

In 1980, the land management authority for Hagemeister Island was transferred by Congress to the US-F&WS when Hagemeister Island became part of the Alaska Maritime National Wildlife Refuge. Prior to 1980, land management authority was with the BLM. Management responsibilities by the respective agencies included annual aerial reindeer and range surveys. During winter 1992, a large proportion of the herd was culled and about 120 animals airlifted to the mainland (see Chapter 6). In autumn 1993, the majority of the herd (about 450 animals) was relocated to the mainland or culled. A few reindeer still remain on the island.

Is There a Scientific Case for Management of Reindeer on Hagemeister Island?

Swanson and Barker (1993) concluded that complete lichen recovery on Hagemeister Island without herd reduction would take approximately 100-150 years. Thus reduction in herd size or removal of entire herd from the Hagemeister Island may be justified if recovery of lichens and preservation of other native flora on Hagemeister Island is the management priority. However, final decisions must be sound and biologically correct.

Productivity and health of the reindeer herd was good despite a high population density and do not support the conclusion that reduced lichen availability on Hagemeister Island had limited population growth. Furthermore, concerns about further die-offs similar to the one in the winter of 1991-1992 appear to have been unjustified (Swanson and Barker 1993) and the large population reduction during autumn 1992 may have been unnecessary. However, this conclusion does not dismiss the need for a more intensive management of the herd to prevent a possible population explosion and subsequent crash. The management stand taken by US-F&WS to extirpate the Hagemeister Island reindeer herd caused a great controversy. In particular, the decision made not to salvage more than 500 carcasses. In the light of the subsistence life-style practiced by a large proportion of Alaskans, this does imply a waste of a valuable resource.

The course of action taken to remove the entire herd is in agreement with the US-F&WS's management policy of Wildlife Refuge Areas. The management purpose of wildlife refuges is "to conserve fish and wildlife populations and habitats in their natural diversity" (J. Strobel pers. commun. 1993). Obviously, the introduced reindeer herd conflicted with this objective. However, it should be kept in mind that reindeer were introduced to Hagemeister Island

before it became a part of the refuge. The objective for the introduction of reindeer on Hagemeister Island was to provide Native people in the village of Togiak with the opportunity to establish a herding industry and an alternative source of meat (see Chapter 1). There was evidence that the village of Togiak had attempted to integrate reindeer into a dynamic subsistence economy.

In the light of the economic and possibly cultural importance of reindeer herding for the Native community, a more "people-oriented" management decision by the US-F&WS (i.e. reduction of herd to about 200 breeding animals and instrumentation of pasture rotation as suggested by Swanson and LaPlant (1987)) would have been more appropriate. This option would have also provided the opportunity to monitor vegetation changes, animal condition, reproductive physiology, and improve our knowledge of management necessary for insular herbivore populations.

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